The CELLULOSE SYNTHASE-LIKE A and CELLULOSE SYNTHASE-LIKE C families: recent advances and future perspectives

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INTRODUCTION

Plant cell walls are complex composites that consist mainly of carbohydrates, including cellulose, hemicelluloses, and pectins (Somerville et al., 2004; Lerouzel et al., 2006; Sandhu et al., 2009; Dobrin et al., 2010; Lipman et al., 2010; Carpita, 2011). The cell walls vary in structure and composition among plant species (Carpita, 2011) and within different cells and tissues of a single plant (Lee et al., 2011). The structural heterogeneity among cell walls is a key factor underlying the functional diversity of plant cell walls (Paula and Kegotra, 2010). Plant cell walls also represent the most abundant source of renewable biomass, and provide materials with a multitude of human uses and other important roles in the biosphere (Paula and Kegotra, 2010; Lee et al., 2011).

Due to the complexity of monosaccharide composition and glycosidic linkages present in plant cell walls, it is predicted that hundreds of enzymes are involved in cell wall carbohydrate biosynthesis (Kegotra and Raikhel, 2001; Scheible and Pauly, 2004). This estimate substantially increases when considering other cell wall-related proteins (Girke et al., 2004; McCann and Carpita, 2008). Spurred by genome sequencing and the availability of powerful comparative and functional genomic tools, the cell wall research community has made significant progress over the last decade in identifying and determining the function of numerous enzymes involved in the synthesis of plant cell wall carbohydrates (Farrokhhi et al., 2006; Lerouzel et al., 2006; Pennig et al., 2009; Sandhu et al., 2009; Dobrin et al., 2010; Lipman et al., 2010). Among these are members of the CELLULOSE SYNTHASE (CESA) superfamily of proteins (Cary GT2; Cantarel et al., 2009). The CESA superfamily includes bona fide CESA proteins involved in cellulose synthesis (Youngs et al., 2007; Endler and Persson, 2011), as well as CELLULOSE SYNTHASE-LIKE (CSL) proteins (Richmond and Somerville, 2000; Hazen et al., 2002; Funcher, 2009) that have been implicated in the synthesis of various β-glucan polymers.

This minireview focuses upon the CSLA and CSLC subgroups, the most divergent CSL subgroups relative to the CESA proteins (Richmond and Somerville, 2000; Youngs et al., 2007). Because members of the CSLA and CSLC subgroups are thought to have evolved through duplication and diversification from a common ancestral gene (Yin et al., 2009; Del Bem and Vincentz, 2010), they share some structural and physicochemical features (Youngs et al., 2007), however they differ in membrane topology and in enzymatic function (Davis et al., 2010). A number of CSLA genes have been shown to encode mannan synthase enzymes that polymerize the 1,4-β-D-glucan backbone of xyloglucans (Cocuron et al., 2007) and possibly other polysaccharides (Dewick et al., 2009). Due to space limitations, we are unable to provide a comprehensive review of these topics; instead we will focus upon some important unanswered questions about the CSLA and CSLC families.

ARE ALL CSLA PROTEINS INVOLVED IN MANNAN SYNTHESIS?

CSLA genes appear to be present in all land plants, and ancestral genes with characteristics similar to CSLA and CSLC sequences have been identified in a number of green algal genomes, in which they are thought to represent a homolog of the progenitor gene from which CSLA and CSLC genes evolved (Del Bem and...
Vincentz, 2010). It has been hypothesized that these CSLA/CSLC-like sequences encode mannan synthases (Yin et al., 2009; Popper et al., 2011), however experimental evidence is needed to test this hypothesis. Heterologous expression of recombinant CSLA proteins has proven particularly effective for determining their enzymatic functions. The involvement of CSLA family members from diverse plant species in the synthesis of 1,4-β-mannan and glucomannan backbones has been demonstrated by a number of studies (Table 1; Dhugga et al., 2004; Liepman et al., 2005, 2007; Suzuki et al., 2006; Goubet et al., 2009, Gille et al., 2011). Studies of recombinant CSLA proteins have further demonstrated that expression of a single CSLA protein in a heterologous host is sufficient to impart enzymatic activity, and that the incorporation of mannose and glucose into glucomannan chains is mediated by a single enzyme (Liepman et al., 2003, 2007; Suzuki et al., 2006; Gille et al., 2011). Since recombinant CSLA proteins from a variety of plants exhibit mannan synthase activity, it is possible that all CSLA proteins are involved in the synthesis of mannan. An alternative possibility is that certain CSLA proteins may catalyze the synthesis of other polysaccharides; in particular a clade of CSLA proteins present only in monocots may have divergent function (Dhugga et al., 2004; Liepman et al., 2007; Del Bern and Vincentz, 2010; Dhugga, 2011). Efforts to characterize members of this clade will provide more information about the biosynthetic capabilities of CSLA proteins. Detailed biochemical studies of CSLA proteins from plants producing mannans of different structures also are needed in order to define whether structural features of these enzymes govern mannann product structure.

**WHAT ARE THE PHYSIOLOGICAL FUNCTIONS OF MANNANS?**

Within plants and algae, mannans are structurally and functionally diverse, and they serve well-known roles as structural elements and as energy reserves (Moreira and Filho, 2008). In angiosperms, mannans are cross-linking glycan that are present at low levels in primary cell walls (Zablackis et al., 1995; Schroder et al., 2009; Marcus et al., 2010), and in greater abundance in secondary cell walls (Handford et al., 2003; Goubet et al., 2009). In gymnosperms, mannans are the most abundant hemicellulosic polysaccharide present in wood (Maeda et al., 2000; Pauly and Keegstra, 2010). Glucomannans also are used for energy storage in corms of plants within the genus Amorphophallus. The AKCSLA3 protein, involved in the synthesis of glucomannan stored in the corms of Konjac, recently has been characterized along with many other sequences encoding proteins involved in other aspects of glucomannan biosynthesis (Gille et al., 2011).

In addition to carbohydrate storage and structure, mannans serve a variety of other functions. In fern roots, mannans are deposited as constituents of cell wall appositions as a defense mechanism to limit microbial ingress (Le Roux et al., 2011). Mannans impart hardness to seeds of some plants, such as tomato species, and they also serve as reservoirs of carbohydrate and as structural elements and as energy reserves.
and lettuce, thereby protecting the embryo and controlling radicle protrusion (Schroder et al., 2009; Buckeridge, 2010). In tomato fruits, mannans also have roles in cell adhesion (Orduz-Ortiz et al., 2009), and recent immunological studies have revealed a much wider distribution of mannans in cell walls than previously appreciated (Marcus et al., 2010). Mannose is an abundant constituent of Arabidopsis trichomes and the CSLA9 gene encoding a glucomannan synthase is among the top one hundred most abundant transcripts present in trichomes (Marks et al., 2008). Mannan epitopes appear to be present throughout trichome cell walls and at trichome bases, indicating that mannans may be involved in trichome to leaf adherence (Figure 1). Mannans also are involved in pollen tube growth, as this process is perturbed in Arabidopsis csla7 mutant plants (Goubet et al., 2003).

A number of studies also implicate mannans within plant developmental signaling pathways. For example, Arabidopsis csla7 mutant embryos exhibit defective embryogenesis, arresting at the globular stage (Goubet et al., 2003), and csla7 mutants have reduced numbers of lateral roots (Zhu et al., 2004). Complementation of the csla7 mutant phenotype has been achieved by overexpression of CSLA9, demonstrating that the CSLA7 and CSLA9 proteins likely make structurally interchangeable mannans in vivo (Goubet et al., 2009). Interestingly, aborted embryos and developmental asynchrony were documented in siliques of transgenic Arabidopsis plants overexpressing various CSLA genes, indicating that mannan abundance influences the progression of embryogenesis (Goubet et al., 2009). A number of other studies have documented growth and developmental responses of plants and cultured plant cells to the application of galactoglucomannan oligosaccharides (GGMOs). For example, GGMOs enhance cell population density and alter the protoxylem:metaxylem ratio of xylogenic cultures of Zinnia (Benova-Kakosova et al., 2006). Treatment of pea stem segments with GGMOs also inhibits auxin-stimulated elongation growth (Austova-Samaiova et al., 1996), possibly through the action of recently discovered mannan transglycosylases (Schroder et al., 2006, 2009). Additional studies are needed to provide more insight about the biological significance of GGMOs and the mechanism of their action.

Efforts to understand the physiological roles of mannans likely have been hindered by functional redundancy, since CSLA genes are members of multiple-gene families in many plants (Richmond and Somerville, 2001; Hazen et al., 2002; Liepman et al., 2007; Roberts and Bushoven, 2007). In Arabidopsis, cila single mutants have been identified for each of the nine CSLA genes (Table 2). Aside from the csla7 mutant, none of these cila single mutants exhibited notable phenotypic abnormalities (Goubet et al., 2009). It seems likely that at least some of the remaining uncharacterized Arabidopsis CSLA proteins also are mannan synthases, however the significant degree of overlap among the expression patterns of these sequences (Mannans et al., 2004; Liepman et al., 2007) probably masks defects resulting from their loss of function in cila single mutants, necessitating the analysis of higher order mutants. One such mutant, the Arabidopsis csla2/csla3/csla9 triple mutant, lacks detectable glucomannan in stems. This glucomannan deficiency did not impact stem strength, indicating that mannans are not required for stem strength in Arabidopsis, or that a compensatory mechanism may exist in their absence (Goubet et al., 2009).

ARE DIFFERENT FORMS OF MANNANS SYNTHESIZED BY DIFFERENT CSL SUBCLASSES?

Recent studies have shed interesting new light on mannan synthesis, by implicating members of the CSLD family in this process (Verherrbruggen et al., 2011; Yin et al., 2011). Analysis
Table 2 | Analyses of csl mutants.

| Mutant name | Gene identifier | Mutant phenotype | Reference |
|-------------|-----------------|------------------|-----------|
| atcsla1     | At4g16590       | No apparent mutant phenotype | Goubet et al. (2009) |
| atcsla2     | At5g22740       | No apparent mutant phenotype | Goubet et al. (2009) |
| atcsla3     | At1g23480       | No apparent mutant phenotype | Goubet et al. (2009) |
| atcsla7     | At3g16650       | Defective embryogenesis, impaired pollen tube growth | Goubet et al. (2009) |
| csld2       | At5g23760       | Reduction of mannose quantity in inflorescence stems | Ubeda-Tomàs et al. (2007) |
| csld3       | At1g23480       | No apparent mutant phenotype | Goubet et al. (2009) |
| csld5       | At5g03760       | Reduction of lateral root formation and rate of growth, decreased efficiency of root-mediated transformation by Agrobacterium tumefaciens | Zhu et al. (2003) |
| csld7       | At4g13410       | No apparent mutant phenotype | Goubet et al. (2009) |
| csld9       | At5g23760       | ~81% reduction of mannose quantity in inflorescence stems | Goubet et al. (2009) |
| csld10      | At1g24070       | No apparent mutant phenotype | Goubet et al. (2009) |
| csld11      | At5g16190       | No apparent mutant phenotype | Goubet et al. (2009) |
| csld14      | At3g56000       | No apparent mutant phenotype | Goubet et al. (2009) |
| csld15      | At4g13410       | No apparent mutant phenotype | Goubet et al. (2009) |
| csld2/3     | At5g22740/At1g23480 | Slight reduction of mannose quantity in inflorescence stems | Goubet et al. (2009) |
| csld2/9     | At5g22740/At5g03760 | Reduction of mannose quantity to trace level in inflorescence stems | Goubet et al. (2009) |
| csld3/9     | At1g23480/At5g03760 | Reduction of mannose quantity to trace level in inflorescence stems | Goubet et al. (2009) |
| csld2/3/9   | At5g22740/At1g23480/At5g03760 | Reduction of mannose quantity below detection level in inflorescence stems | Goubet et al. (2009) |

DO THE CSLCs ENCODE XYLLOGLUCAN GLUCAN SYNTHASES? 

Like the CSLAs, CSLC sequences have been found in many extant species of Viridiplantae, spanning several divisions, including Magnoliophyta, Lycopodiphyta, Bryophyta, and Charophyta (Del Bem and Vincentz, 2010). Within angiosperms, CSLGs have been found in all species surveyed thus far (Yin et al., 2009; Del Bem and Vincentz, 2010), including three species that have been used as models to investigate CSLC function: nasturtium (T.moellendorffii), Arabidopsis (Arabidopsis thaliana), and barley (Hordeum vulgare). The first evidence that xyloglucan glucan synthase (XGS) might be encoded by a member of the CSLC family was provided by Cocuron et al. (2007) using a comparative genomics approach. Using nasturtium (Tropaeolum majus) seeds, which utilize xyloglucan as the primary seed storage polysaccharide (Cislaghi et al., 1991), transcriptional profiling was used to identify genes preferentially expressed during the stage of seed development when xyloglucan deposition occurs. The only CSL gene transcripts detected by this analysis were those of the TmCSLC gene, a homolog of Arabidopsis CSL4 (AtCSLC4). Transgenic Pichia pastoris cells expressing the TmCSLC or AtCSLC4 protein produced soluble 1,4-β-glucans with a low degree of polymerization.
White et al., 1993). Although Cocuron et al. (2007) show that there is a strong correlation between the expression of Arabidopsis CSLC4 and a xyloglucan xylosyltransferase (AtXXT1) belonging to clade 2, AtCSLC4, 5, 8, and HvCSLC3 belong to clade 1. Dwivany et al. (2009) concluded that there is insufficient evidence to assign functions to HvCSLC1 and HvCSLC4. However, the authors propose that HvCSLC2 likely is not involved in xyloglucan biosynthesis, and instead suggest that it may be involved in cellulose biosynthesis. Although the conclusions reached by Dwivany et al. (2009) are plausible, additional evidence from heterologous expression and mutant genetic studies would strengthen their arguments.

In contrast to using an experimental system in which a significant portion of the hemi-cellulose present is xyloglucan, Dwivany et al. (2009) studied CSLCs of barley (Hordeum vulgare L.), where xyloglucan is a minor cell wall component (Sakurai and Masuda, 1978; Kato et al., 1981; Fincher, 1993). The authors identified and characterized four barley CSLCs, HvCSLC4–7 (a fifth, HvCSLC5 also was identified but not characterized). Phylogenetic analysis of CSL family members from several eudicots and monocots, Phycomitrella patens, Selaginella moellendorffii, and Chara globularis indicates that the CSLC family contains four clades: HvCSLC1–4 and AtCSLC1–4, belonging to clade 2. Phycomitrella and Selaginella CSLCs comprise clade 3, and AtCSLC6 belongs to clade 4. In addition to taxonomic relationships having an effect on tree structure (i.e., clade 3), the authors hypothesize that when considered in conjunction with the biochemical and molecular evidence (discussed below), the structure of the phylogenetic tree may show functional specialization, with members of clades 2 and 4 having GS and XGS activities, respectively. Based on results of transcriptional profiling of barley organs and tissues, coexpression analysis of HvCSLC1 and HvCSLC3 transcripts, the CSLC proteins immunolocalize to the plasma membrane in immuno-EM and membrane fractionation experiments. Based on results from these experiments and the molecular characterization at the gene and transcript levels, Dwivany et al. (2009) conclude that there is insufficient evidence to assign functions to HvCSLC1 and HvCSLC4. However, the authors propose that HvCSLC2 likely is not involved in xyloglucan biosynthesis, and instead suggest that it may be involved in cellulose biosynthesis. Although the conclusions reached by Dwivany et al. (2009) are plausible, additional evidence from heterologous expression and mutant genetic studies would strengthen their arguments.

In addition to genetic redundancy and lethality, determining the effects upon polysaccharide content in cole mutants could pose a significant challenge if members of the CSLC family are involved in cellulose biosynthesis. One potential difficulty would be the inability to distinguish between cellulose synthesized by CSLCs versus CESA5s. Another would be determining if changes in amorphous or crystalline cellulose are due directly to the mutation or are the result of a secondary response to the mutation. Keeping these challenges in mind, detailed studies of such mutants, coupled with biochemical studies of recombinant CSLC proteins ultimately are expected to provide the evidence needed to conclusively define the function(s) of many CSLC family members.
and CSLC proteins and the synthesis of plant polysaccharides in general.

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REFERENCES

Austrova-Sumepova, O., Liskova, D., Kakenova, D., Kaladov, M., Karacsonyi, S., and Balins, L. (1996). Inhibition of auxin-stimulated short-term elongation growth of pea stem segments by galactoglucomannan isolated from oat germs. J. Plant Physiol. 147, 611-613.

Benova-Rakova, A., Dignietier, C., Gruber, F., Ramchandran, P., Jasenea, A., Popnet, E., Barbo, O., Zhang, Z., Capo, F., Dupre, F., Lison, D., and Gellert, D. (2006). Galactoglucomannans increase cell population density and alter the proteome of tomato trichome cell types in tobacco cultivars of thirteen species. Physiol. Plant. 142, 506-709.

Benedetti, A. T., Cao, C.-M., Matulli, M., Jomot, J. K., Hoa, G., Blancko, C., Sonesson, L., Blenckner, E. R., Schiller, K. V., and Wällin, W. G. (2008). Functional analysis of the cellulose synthase-like C family encodes a P-1,4 glucan synthase. Proc. Natl. Acad. Sci. U.S.A. 105, 8705-8709.

Bendix, J., Brandizzi, F., Liepman, A. H., Lerouxel, O., and Keegstra, K. (2010). Arabidopsis mutant CSLA4 and CSLC4 have opposite orientations in the Golgi membranes. Plant Mol. Biol. 70, 1027-1037.

Bel, B. M., and Vosmiet, M. G. (2010). Evolution of teloglucomannan-related genes in plants. BMC Evol. Biol. 10, doi:10.1186/1471-2148-10-341.

De Schutter, K., Lin, Y.-C., To, P., Van Hocke, A., Gilika, S., Nibbering-Lehmann, J., Ronen, P. Van den Peet, Y., and Callewaert, N. (2009). Genome sequence of the recombinant protein production host Pichia pastoris. Nat. Biotechnol. 27, 276.

Drugg, K. S. (2011). Biosynthesis of non-cellulosic polysaccharides of plant cells. Phytochemistry 74, 1-19.

Drugg, K. S., Barraturo, R., Whitten, B., Stocka, K., Handbrook, J., Randhawa, G. S., Dolan, M., Knapp, A. J., Tomes, D., Nicholls, S., and Anderegg, P. (2004). Great seed β-mannan synthase is a member of the cellulose synthase super gene family. Science 303, 905-908.

Dehlin, M., Potrofins, F., and Bacic, A. (2010). Plant cell walls: the deconstruction of the plant wall. Funct. Plant Biol. 37, 357-381.

Gillis, S., Cheng, K., Shimer, M. E., Liepman, A. H., Wilkeron, C. P., Gupta, A. P., Miller, D. W., Lang, P., Dentini, C., Concetti, V., Edwards, M., Facetti, C., and Reid, J. S. (1991). Structure and solution properties of unnatural polysaccharide. Carbohydr. Res. 214, 299-314.

Gillis, M. J., Liñérd, P. J., Bowld, D. W., Lang, P., Dentini, C., Concetti, V., Edwards, M., Facetti, C., and Reid, J. S. (1999). Cell wall biology: perspectives on cell wall biogenesis. Frontiers in Plant Science 6, 219-227.

Keegstra, K., Raikhel, N. V., and Wilkeron, C. P. (2011). Plant Glucosyltransferases. Curr. Opin. Plant Biol. 14, 219-224.

Kim, C. M., Park, S. H., Je, B. I., Park, S. H., Park, S. J., Piao, H. L., Eun, M. Y., Dolan, L., and Han, C. D. (2007). OvCSD1, a Cellulose Synthase-Like gene involved in the synthesis of the hemi-cellulose glucamannan. Plant Physiol. 145, 513-524.

Gitter, T., Laustren, J., Tran, H., Keegstra, K., and Raikhel, N. (2004). The Cell Wall Navigator database: a systems-based approach to organism-unrestricted mining of proteins related to cellulose metabolism. Plant Physiol. 136, 3005-3008.

Goodin, D. M., Shu, S., Howson, R., Neupane, B., Hesse, R. F., Fano, J., Mitrani, T., Dirks, W., Hollow, U., Pattani, N., and Robinson, D. S. (2012). Phytosystem: a comparative platform for green plant genomics. Nucleic Acid Res. 41, D1078-D1086.

Goodfellow, M. G., Bubum, T. C., Goubet, A. F., Prime, T., A. M., Miles, S. J., and Dupre, P. (2003). CALS5, a cellulose synthase-like putative glycosyltransferase, is important for pollen tube growth and embryogenesis in Arabidopsis. Plant Physiol. 131, 547-557.

Hamann, T., Osborne, E., Youngs, H., Meijer, M., Nausser, E., and Somerville, C. (2004). Global expression analysis of CESA and CSL genes in Arabidopsis. Cellulose 11, 279-288.

Handford, M. G., Arabia, T. C., Goubet, A. F., Prime, T. A., Miles, S. J., Yu, X., and Dupre, P. (2005). Identification and characterization of cell wall mannans polysaccharides in Arabidopsis thaliana. Planta 221, 27-38.

Hansen, P. S., Scott-Craig, J. S., and Walten, J. D. (2002). Cellulose synthase-like (CSL) genes in rice. Plant Physiol. 130, 546-548.

Hata, Y., Ik, K., and Matsumoto, K. (1981). Cell-wall polysaccharides of immature barley plants. II. Characterisation of a xyloglucan. Agric. Biol. Chem. 45, 2753-2757.

Keegstra, K., Raikhel, N. V., and Wilkeron, C. P. (2011). Plant Glucosyltransferases. Curr. Opin. Plant Biol. 14, 219-224.

Kim, C. M., Park, S. H., Je, B. I., Park, S. H., Park, S. J., Piao, H. L., Eun, M. Y., Dolan, L., and Han, C. D. (2007). OvCSD1, a Cellulose Synthase-Like gene involved in the synthesis of the hemi-cellulose glucamannan. Plant Physiol. 145, 513-524.

Gitter, T., Laustren, J., Tran, H., Keegstra, K., and Raikhel, N. (2004). The Cell Wall Navigator database: a systems-based approach to organism-unrestricted mining of proteins related to cellulose metabolism. Plant Physiol. 136, 3005-3008.

Goodin, D. M., Shu, S., Howson, R., Neupane, B., Hesse, R. F., Fano, J., Mitrani, T., Dirks, W., Hollow, U., Pattani, N., and Robinson, D. S. (2012). Phytosystem: a comparative platform for green plant genomics. Nucleic Acid Res. 41, D1078-D1086.
lies in cell adhesion in tomato fruit pericarp parenchyma. Mol. Plant 2, 910–921.

Park, S., Suzuki, A. L., Gu, F., Guo, F., and Nelson, E. (2011). A role for CSLD during cell-wall synthesis in apical meristem of tip-growng root hair cells. Nat Cell Biol. 13, 973–980.

Patterson, B. W., Hanner, C. T. III., Yang, B., Broida, A. D., Dougall, C. K., Olkk, A. T., Vermeer, W., Kiek, E. E., McCarty, D. R., Davies, M. F., Thomas, S. R., McCann, M. C., and Carpita, N. C. (2009). Genetic resources for maize cell wall biology. Plant Physiol. 151, 1705–1729.

Pepper, Z. A., Michel, G., Harve, C., Donohue, D. S., Willans, W. G., Tastly, M. G., Kleinig, B., and Stenu, D. (2011). Evolution and diversity of plant cell walls from algae to flowering plants. Annu. Rev. Plant Biol. 62, 767–790.

Pepino, P. M. (1980). Cooperative action of fungal cellulase and UDP-sugar xyloglucan transglucosidase in the synthesis of fungal-like polysaccharide. Biochem. Biophys. Acta 64, 605–612.

Richmond, T., and Somerville, C. R. (2005). Hemicelluloses: an update. Annu. Rev. Plant Physiol. 56, 485–488.

Richmond, T. A., and Somerville, C. R. (2008). The cellulose synthase superfamily: recent advances and future perspectives. Front. Plant Sci. 9, 131–143.

Sakurai, N., and Masuda, Y. (1978). Distribution and characterization of chitin in cell adhesion in tomato fruit pericarp parenchyma. Mol. Plant 2, 910–921.

Schroder, R., Atkinson, R. G., and Redgwell, B. J. (2009). Re-interpreting the role of endo-β-mannanase as mannan-endotransglycosylase in the plant cell wall. Ann. Bot. 104, 197–204.

Schreiber, R., Weymann, T. F., Sharma, N. N., and Atkinson, R. G. (2006). LeMAN4 endo-β-mannanase from snapdragon fruit can act as a mannan transglycosylase or hydrolase. Plant Biotechnol. 22, 1001–1002.

Shen, T., Erhardt, C., and Reinhold, T. F., Sharma, N. N., and Atkinson, R. G. (2012). The cellulose synthase superfamily of Arabidopsis thaliana leaves. BMC Plant Biol. 9, doi: 10.1186/1471-2229-9-9.

Shigen, H. S., Hamann, T., Osborne, E., and Somerville, C. R. (2007). A new method for iso-9. doi: 10.1186/1471-2229-9-9.

Suzuki, S., Li, L., Sun, Y. H., and Zhang, Y. L. (2006). The cellulose synthase gene superfamily and biochemical functions of xylan-specific cellulose synthase-like enzymes in Populus trichocarpa. Plant Physiol. 142, 1253–1264.

Takeda, V., Peraldi, A., Weslbad, F., Nicholson, F., Drontan, J. H., and Vain, P. (2012). DNA-mutation in Buchloeidopsis dityosoma. J. Exp. Bot. 63, 567–576.

Takeda, V., Weslbad, F., Wright, J., Bower, M. W., and Vain, P. (2010). Distribution and characterization of more than 1000 T-DNA tags in the genome of Buchloeidopsis dityosoma community standard line Bdr1. Plant Biol. 12, 785–797.

Ueda, T., Yasuda, Y., Iioka, Y., Trudet, S., Yasuda, Y., Takada, H., Iwata, S., Naka, T., Takeda, Y., and Atkinson, R. G. (2006). The cellulose synthase superfamily: recent advances and future perspectives. Front. Plant Sci. 9, 131–143.

White, A. R., Xin, Y., and Ponzeh, V. (1993). Xyloglucan hydrolysis in Golgi membranes from Phloem sap (ps). Biochem. J. 294, 231–238.

Yin, L., Verhaarrebron, Y., Okisaka, A., Matsuwuii, C., Kuem, R., Fuji, L., Jensen, J. K., Kniv, J. F., Auer, M., Williams, W. G., and Scheller, H. V. (2012). The cooperative activities of CSLCs, CSLD3, and CSLD5 are required for normal Arabidopsis development. Mol. Plant 5, 1026–1037.

Yin, Y., Huang, J., and Yu, Y. (2009). The cellulose synthase superfamily is not directly affected by sugars. BMC Plant Biol. 9, doi: 10.1186/1471-2229-9-9.

Yoon, S. S., Hamann, T., Osborne, E., and Somerville, C. R. (2007). "The cellulose synthase superfamily," in Cellulose: Molecular and Structural Biology, eds M. Brown and I. M. Smithen (Berlin: Springer), 35–49.

Zielinski, E., Huang, J., Darville, A. G., and Elbein, P. A. (1995). Characteristics of the Drosophila melanogaster cellulose synthase genes. Plant Physiol. 107, 1129–1135.

Zhu, V., Nieu, L., Poppert, Z. A., Michel, G., Facette, M., Hamann, T., Milne, J., Osborne, E., Pardoe, A., Petron, S., Raab, T., Verker, S., and Yung, H. (2004). A systems approach to understanding plant cell walls. Science 305, 229–231.