Release, Recycle, Rebuild: Cell-Wall Remodeling, Autodegradation, and Sugar Salvage for New Wall Biosynthesis during Plant Development

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http://dx.doi.org/10.1016/j.molp.2017.08.011

ABSTRACT

Plant cell walls contain elaborate polysaccharide networks and regulate plant growth, development, mechanics, cell-cell communication and adhesion, and defense. Despite conferring rigidity to support plant structures, the cell wall is a dynamic extracellular matrix that is modified, reorganized, and degraded to tightly control its properties during growth and development. Far from being a terminal carbon sink, many wall polymers can be degraded and recycled by plant cells, either via direct re-incorporation by transglycosylation or via internalization and metabolic salvage of wall-derived sugars to produce new precursors for wall synthesis. However, the physiological and metabolic contributions of wall recycling to plant growth and development are largely undefined. In this review, we discuss long-standing and recent evidence supporting the occurrence of cell-wall recycling in plants, make predictions regarding the developmental processes to which wall recycling might contribute, and identify outstanding questions and emerging experimental tools that might be used to address these questions and enhance our understanding of this poorly characterized aspect of wall dynamics and metabolism.

Key words: Plant cell walls, wall degradation, wall recycling, wall biosynthesis


INTRODUCTION

Plant cell walls are complex extracellular matrices that control the growth and morphology of plants at the cellular, tissue, and organismal levels, determine the mechanical properties of plant tissues, regulate cell-cell adhesion, and serve as sensory interfaces between plants and their environment (Somerville et al., 2004). Plant cell walls are composed of cellulose (multiple chains of β-(1,4)-D-glucan) and other glucans, including callose (β-(1,3)-D-glucan) and mixed-linkage β-(1,3)-(1,4)-D-glucan (MLG) that are produced at the plasma membrane, hemicelluloses and pectins that are produced in the Golgi and delivered to the apoplast by secretory vesicles (Mohnen, 2008; Wilson et al., 2015), structural glycoproteins, enzymes, ions, and water. All growing plant cells produce primary walls that are dynamically modified, reorganized, and loosened to allow for wall relaxation and controlled cell expansion (Cosgrove, 2005).

Primary cell walls can be divided into type I or type II walls based on composition. Type I cells walls are found in eudicots, noncommelinoid monocots, and gymnosperms, whereas type II walls are restricted to commelinoid monocots, including grasses (Vogel, 2008). Type I and type II primary walls have similar amounts of cellulose, but hemicelluloses make up a greater proportion of type II walls than of type I walls, which is offset by higher pectin content in type I walls. Type I walls also have higher proportions of structural proteins than type II walls. Hemicellulose composition differs between wall types, with hemicellulose in type I walls largely consisting of xyloglucan (XyG) with small amounts of glucomannans and glucuronoxylans, and with hemicellulose in type II walls being mostly glucuronorabinoxylans (GAX) with smaller amounts of MLG and xyloglucan (XyG) (Vogel, 2008). Type II walls also contain hydroxycinnamic acids that associate with GAX (Vogel, 2008; Rennie and Scheller, 2014).

Cell-wall polysaccharides are polymerized by glycosyltransferases (GTs) that use nucleotide diphosphate-sugar (NDP-sugar) substrates, which are generated from soluble sugarphosphates (Yin et al., 2011). UDP-glucose is the direct substrate for the synthesis of glucans present in the cell wall, including cellulose,
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colloid, XyG, which comprises a β-(1,4)-D-glucan backbone with neutral sugar sidechains (Fry, 1989), and MLG. UDP-glucose also acts as a metabolic nexus in de novo NDP-sugar synthesis, in that it can be converted to other NDP-sugars by a suite of enzymes for the synthesis of non-glucan polysaccharides (Bar-Peled and O’Neill, 2011). In a phylogenetic study of plant nucleotide-sugar interconversion enzymes (NSE), Yin et al. (2011) found that all 11 NSE families present in vascular plants are encoded in the genomes of early-diverging land plants such as moss, as well as in algal genomes. Despite differences in wall polysaccharides and composition across plant taxa, high NSE conservation indicates that the activation and utilization of each of these sugars for cell-wall production is favored by natural selection. Furthermore, the different biosynthetic sites for different classes of wall polysaccharides necessitate specific subcellular distributions of sugars, sugar phosphates, NDP-sugar transporters, and NSEs to provide a multitude of GTs with their NDP-sugar substrates (Rautengarten et al., 2014, 2016,2017).

It is estimated that 10%–15% of the genes encoded in the Arabidopsis genome function in cell-wall assembly or modification (Carpita et al., 2001). Furthermore, the rate of annual global carbon fixation by plants is estimated to be \( \sim 2.34 \times 10^{17} \) g per year (Geider et al., 2001), with approximately 45% of that fixed carbon destined for incorporation into plant cell walls (Field et al., 1998). These estimations indicate that plant cell walls represent the most prominent energy and carbon sink in nature. Although cell walls are sometimes envisioned as recalcitrant, static exoskeletons that simply provide structural support, they embody significant amounts of energy-rich sugars and are a potentially rich carbon resource for plants undergoing rapid growth and developmental transitions. This raises the question of to what extent plants recycle the energy stored within their cell walls to optimize metabolic flux during growth and development. Here, we explore this question from the past through the future, describing what is currently known about the dynamics of cell-wall recycling in plants and discussing the developmental processes to which cell-wall recycling might contribute. We apologize in advance to colleagues whose work is not cited due to space limitations.

A BRIEF HISTORY OF CELL-WALL RECYCLING RESEARCH IN PLANTS

Inspired by work in bacterial and fungal systems, Lee et al. (1967) first observed the autolysis and solubilization of plant cell-wall material isolated from maize (Zea mays) seedlings (Lee et al., 1967). This pioneering work challenged the idea that plant cell walls act solely as recalcitrant, fixed structures and suggested that wall material could be degraded by endogenous mechanisms. Later work revealed a range of autolytic activities in cell-wall material prepared from maize coleoptiles fed with \(^{14}C\)-glucose that were consistent with endo- and exo-arabinase, xylanase, galactanase, polygalacturonanase, and mannanase activities (Nock and Smith, 1987). Observations of \(^{-}[U-{\,}14C]glucose and \(^{-}[U-{\,}14C]arabinose incorporation into soluble and cell-wall polymers of proso millet (Panicum miliaceum L. cv Abarr) liquid culture cells and maize leaves indicated the existence of a sugar salvage pathway that glean storage sugars and produces storage-1-phosphates and NDP-sugars that can be used for wall synthesis (Gibeaut and Carpita, 1991). Long-term radiolabel tracing experiments revealed that sugars are constantly recycled, albeit with differing kinetics, from the cell wall via polysaccharide turnover and re-synthesis (Gibeaut and Carpita, 1991). These studies discovered a previously unknown biological function for plant cell walls: the primary cell wall is not simply a carbon sink but rather is a dynamic compartment that actively turns over to recycle wall-bound carbon resources and support plant growth and development. Despite the realization of this facet of the biology of plant cell walls, remarkably little is known about the processes controlling cell-wall recycling as a mechanism to re-incorporate degraded wall material into new wall components through modification and metabolic salvage, and the functional importance of these metabolic pathways in plant development. We classify wall-recycling mechanisms into two main categories: “in muro recycling,” which does not require sugar internalization, conversion to NDP-sugar substrate, or GT activity, and “metabolic recycling,” which requires these steps.

Cell-Wall Autodegradation and Recycling Review

IN MURO POLYSACCHARIDE RECYCLING VIA TRANSGLYCOSYLATION

Recycling, by definition, is the conversion of “waste” into reusable material. Although cell walls do not contain waste material per se, some wall materials are likely to be more biologically and mechanistically dispensable than others, based on polysaccharide interactions, growth requirements, and the developmental stage of the plant cell. Plants can actively cleave and re-link wall polysaccharides in muro (Figure 1) to influence wall structure and mechanics. Enzymes that cleave a donor polysaccharide and ligate one of the degradation products onto a different acceptor molecule are referred to as transglycosylases. Multiple classes of endogenous plant transglycosylases have been identified that can act on different hemicellulosic and glucan substrates (for a comprehensive review of transglycosylases, see Franková and Fry, 2013). Transglycosylation is an important aspect of cell-wall recycling, since it allows for the direct repurposing of glycan cleavage products to construct newly linked wall polymers.

The XyG endotransglycosylase/hydrolase (XTH) family of enzymes hydrolyzes and reconnects XyG fragments via XyG endotransglycosylase (XET) activity (Figure 1) (Shinohara et al., 2017). Thus, XTHs can elongate glucan chains without consuming NDP-sugars, which are likely scarce in the apoplast. Incubating plants with fluorescent sulforhodamine-conjugated XyG oligosaccharide (XGO) probes demonstrates that exogenous XyG fragments are incorporated into tissues with high XET activity, such the elongation zones of Arabidopsis and tobacco roots (Vissenberg et al., 2000). Apoplastic XyG incorporation has also been observed in rapidly expanding regions of excised pea stems (Warneck et al., 1998). Application of intact XyG to pea stens reduces wall extension and increases wall stiffness, likely due to tethering of large XyG fragments via XET activity, but incubation with small XGOs encourages growth and wall flexibility at higher concentrations (Takeda et al., 2002). Takeda et al. (2002) attribute the loosening effects of XGOs to XET-mediated XyG chain shortening. Non-fucosylated XGO also accelerates growth and cell division of tobacco XD-6 suspension culture cells but...
increases the size of XyG molecules, indicating that XETs can also elongate XyG chains and simultaneously promote growth (Kaida et al., 2010). In addition, XTH family members from Arabidopsis, barley (Hordeum vulgare), and Equisetum species show expanded functionality and can catalyze the hetero-transglycosylation of XyG donors onto cellulosic acceptors with low activity (Maris et al., 2011), cellulosic and XyG donors onto XyG and MLG acceptors (Hrmova et al., 2007), and MLG donors onto XyG acceptors (Simmons et al., 2015). A recent characterization of AtXTH3 revealed yet another novel activity that mediates homo-transglycosylation of cellulosic donors onto cellulose acceptors (Shinohara et al., 2017). This repertoire of endotransglycosylase activities appears to enable plants to directly re-incorporate numerous cell-wall glucans for new purposes and tune polysaccharide lengths, interactions, and linkages during development.

Drawing a parallel with XET enzymes, Franková and Fry (2011) conducted an extensive investigation of degradative activities in protein extracts from 57 rapidly growing plant organs from 16 species and identified the presence of numerous xylan-related transglycosylase enzymes including trans-β-xylanase (Figure 1), trans-β-xylosidase, trans-α-xylosidase, trans-α-arabinanase, and trans-α-arabinosidase (Franková and Fry, 2011). These enzymatic studies indicated that xylan transglycosylation can occur using mono (exo-transglycosylase activity)- and oligo (endo-transglycosylase activity)-saccharide donors, whereas XET activity favors oligosaccharide donors. Information on the exact activities and sources of transglycosylase activities resulting from this study can be found in the searchable GHATAbase (glycosylhydrolase and transglycosylase activity database) (Franková and Fry, 2011). Xylan endotransglycosylase activity has also been detected across a variety of monocots and eudicots (Johnston et al., 2013). A xylan endotransglycosylase gene, PtxtXyn10A, affects cell-wall structure and growth in hybrid aspen (Populus tremula × tremuloides), demonstrating the broad conservation of xylan endotransglycosylase activity across angiosperm phyla and plant tissues (Derba-Maceluch et al., 2015). The ubiquity of hemicellulose transglycosylases implies their importance for cell-wall remodeling and recycling.
During growth and development, metabolic tracing and biochemical characterization of transglycosylase-liable polysaccharides will be required to confirm their specific fates and effects during in muro wall recycling.

**AUTODEGRADATION OF PRIMARY CELL WALLS**

In addition to in muro recycling, metabolic recycling of wall components in plants can also occur via polysaccharide autodegradation, internalization of cleavage products, metabolic salvage and generation of new NDP-sugars, and synthesis of new wall polymers (Figure 2). The relative contributions of in muro and metabolic wall recycling to plant development are unknown, but endogenous mechanisms of autodegradation and metabolic sugar salvage are common in plants (Bar-Peled and O'Neill, 2011) and likely play a dominant role in wall recycling. Polysaccharides can be autodegraded by endolytic enzymes that cleave in the middle of polysaccharides (glycanases), or exolytic enzymes that cleave single sugars from the non-reducing ends of polysaccharides (glycosidases; Figure 2A) (Lopez-Casado et al., 2008). Plants possess over 20 known glycosylhydrolase (GH) activities, specific for particular linkages found in wall polysaccharides (Minic and Jouanin, 2006; for a review of structure-function relationships of various wall-degrading enzymes, see Gilbert, 2010). Within the XTH family, most characterized enzymes exhibit XET activity. However, some
XTHs solely act as XyG endohydrolases (XEHs), hydrolyzing XyG into XGOs (Shinohara et al., 2017). Studies of XEHs indicate that XyG trimming by exohydrolases after delivery to the apoplast determines final XyG composition and degree of polymerization. Residues of XyG sidechains can be removed by the \( \alpha-(1,2) \)-fucosidase AtFUC95A/AXY8 (Léonard et al., 2008; Günl et al., 2011), the \( \beta-(1,2) \)-galactosidase AtBGAL10 (Sampedro et al., 2012), and the \( \alpha-(1,6) \)-xylosidase AtXYL1/AXY3 (Sampedro et al., 2001, 2010; Günl and Pauly, 2011), all of which apoplastically degrade XyG. Recently, soluble and membrane-associated \( \beta \)-glucosidases capable of cleaving the XyG backbone (AtBGLC1 and AtBGLC3, respectively) were characterized (Sampedro et al., 2017). Together, this work suggests that hydrolyzed XyG fragments are destined for further degradation into monosaccharides for metabolic reaction through salvage pathways.

In addition to XyG-degrading enzymes, xylanase activity has been detected in cell-wall material derived from maize coleoptiles, potentially enabling cell-wall loosening and expansion (Nock and Smith, 1987). Xylan-degrading enzymes have been characterized less extensively than those for XyG in plants, despite being relatively well studied in plant pathogens (Maino et al., 1974; Briot et al., 2006; Dodd et al., 2011; Déjean et al., 2013; Santos et al., 2014). Thus far, endogenous xylanases, including endo-\( \beta-(1,4) \)-xylanases, \( \beta-D \)-xylosidases, and \( \alpha-L \)-arabinofuranosidases have been identified in Arabidopsis stems (Suzuki et al., 2002; Goujon et al., 2003; Minic et al., 2004; Ichinose et al., 2010), poplar tension wood (Populus tremula \( \times \) P. alba) (Decou et al., 2009), and papaya fruit (Carica papaya L.) (Chen and Pauly, 2003). Although not originally thought to be present, endogenous \( \beta \)-glucuronidase activity has been reported in plants such as sugarbeet (Beta vulgaris) (Alwen et al., 1992; Wozniak and Owens, 1994). Additional xylan-degradative activities are also described in the GHFABase (Frankova and Fry, 2011). Plant-encoded xylanase inhibitor proteins that are thought to inhibit fungal xylanases have also been discovered (Figure 2A) (Fierens et al., 2003; Vasconcelos et al., 2011). Whether or not plant xylanase inhibitor proteins control plant development by regulating wall autodegradation remains to be determined.

Pectin degradation processes have also been well characterized in plants (Figure 2A) (Mohnen, 2008). Pectins are acidic polysaccharides that function in numerous wall degradation-related processes such as cell elongation, organ separation, cell-cell adhesion, and tissue mechanics, and contain the greatest diversity of monosaccharides and glycosyl linkages in the cell wall (Mohnen, 2008). Pectins are synthesized in the Golgi and primarily consist of three domains: homogalacturonan (HG), rhamnogalacturonan-I (RG-I), and rhamnogalacturonan-II (RG-II). HG makes up the majority of pectin in the wall and consists of \( \alpha-(1,4) \)-galacturonic. HG is secreted with most of its galacturonic acid residues methylsterified at the C6 position; these methyl-ester groups can be removed by pectin methylesterases (PMEs) that act in processive or non-processive fashions to reveal carboxyl groups on galacturonic acid residues, which affect the charge of the wall and the susceptibility of HG to enzymatic degradation (Micheli, 2001). PME inhibitor proteins (PMEIs) regulate PME activity, and PME genes often encode N-terminal PMEI domains, which are thought to prevent premature PME activity. Methylation-esterified HG is resistant to degradation, whereas de-methyl-esterified HG is susceptible to two different types of pectin-degrading enzymes known as polygalacturonases (PGs), which hydrolyze the HG backbone in endo- or exo-fashion, and pectate lyases (PLs), which cleave the HG backbone via \( \beta \)-elimination (Senechal et al., 2014). Polygalacturonase inhibitor proteins (PPIPs) can inhibit fungal PGs but might also regulate plant PG activity (Kalunke et al., 2015). Families of pectin-degrading genes are notably large in plants; for example, Arabidopsis is predicted to encode approximately 69 PGs (González-Carranza et al., 2007; Cao, 2012), 26 PLs (Palusa et al., 2007; McCarthy et al., 2014), 66 PMEs (Wolf et al., 2009; McCarthy et al., 2014), and 69 PMEIs (Wolf et al., 2009), implying numerous functions for pectins in cell walls and complex regulation of pectin abundance and properties throughout development. It is curious that despite the many examples of hemicellulose transglycosylation, pectin transglycosylation has not been detected (Figure 1).

Although HG-degrading enzymes are well characterized, little is known about if or how plants degrade the intricate linkages present in RG-I and RG-II. A recent groundbreaking discovery of the ability of a human gut microbe, Bacteroides thetaiotaomicron, to cleave 20 of the 21 known linkages in RG-II further opens avenues for exploring how plants might degrade their walls and mobilize wall-bound sugars (Ndeh et al., 2017). Ndeh et al. (2017) report the identification of seven new GH families (GH137–143); which if present in plant genomes would imply that plants might autodegrade RG-II. These data also evoke the idea that plants might benefit from microbes, particularly endophytes, if these microbes break down complex wall carbohydrates and release soluble sugars that can be salvaged by the plant, although this idea requires further evidential support.

Due to its hydrogen-bonded multi-chain structure, cellulose is mechanically strong and much more recalcitrant to degradation than most matrix polysaccharides; despite this, cellulose degradation appears to be a vital process for plant development. Plants encode several types of cellulose-degrading enzymes (Figure 2A), including endo-\( \beta-(1,4) \)-glucanases (Park et al., 2003), exo-\( \beta-(1,4) \)-glucanases (cellobiohydrolases), and \( \beta \)-glucosidases (Wilson et al., 2015). Early studies showed that antibody-mediated inhibition of endoglucanase activity increased the breaking strength of abscission zones in bean and maize, indicating that \( \beta-(1,4) \)-glucan (cellulose, XyG, MLG) degradation is important for controlled cell separation (Levy et al., 2002). An interesting yet seemingly paradoxical aspect of cellulose biosynthesis is that a member of the GH9 family of endo-\( \beta-(1,4) \)-glucanases known as KORRIGAN is required for normal cellulose biosynthesis in Arabidopsis (Lei et al., 2014; Vain et al., 2014) and poplar (Populus alba x grandidentata) (Maloney and Mansfield, 2010). KORRIGAN and other \( \gamma \)-subfamily endo-\( \beta-(1,4) \)-glucanases have a transmembrane domain that might anchor the protein to the plasma membrane and help it cleave nascent cellulose chains during biosynthesis.
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perhaps as part of an “editing” process (Lei et al., 2014; Vain et al., 2014), whereas α- and β-subfamilies are thought to be secreted to the apoplast (Libertini et al., 2004). PopCel1 and PopCel2 are poplar (Poplar alba L.) endo-β-(1,4)-glucanase genes important for normal leaf growth and cellulose biosynthesis, and also release cellulose- and xyloligocarbohydrate oligosaccharides from wall preparations of suspension culture cells, further indicating that glucanase activities balance cell-wall biosynthesis and degradation (Ohmiya et al., 2000, 2003; Park et al., 2003).

As highlighted above, hydrolytic polysaccharide degradation is a tightly controllable mode of wall autodegradation. However, another type of degradation might also occur for wall polysaccharides. Oxido-reductases (peroxidases) and laccases are responsible for free-radical-coupled lignin polymerization during secondary wall formation. These peroxidases and laccases, and/or other redox-active enzymes, might also generate reactive oxygen species (ROS) that causes oxidation-mediated polysaccharide cleavage in primary cell walls (Nersisian et al., 1998) (Figure 2A). In vitro proof-of-concept work demonstrated that application of H2O2 triggers scission of various polysaccharides including arabinogalactan, cellulose, polygalacturonic acid, and xylan (Miller, 1986). Fry (1998) showed that in vitro cleavage of XyG is mediated through oxidative cleavage by superoxide radical derived from O2−, the presence of a transition metal such as Cu2+, and an electron donor (Fry, 1998). This mechanism opens the possibility of in situ oxidative scission of wall polysaccharides in living plant tissues (Fry, 1998). Indeed, at least two peroxidases are known to function in Arabidopsis root elongation (Passardi et al., 2006). Addition of exogenous H2O2 to rice roots has been shown to promote cell expansion through modification of pectin biosynthesis and HG de-methylation, suggesting that ROS and enzymatic cell-wall loosening might act synergistically in planta, although this has not been studied with endogenous ROS levels (Xiong et al., 2015). Recent interest has emerged surrounding the ability of microbial lytic polysaccharide monoxygenases and other sources of external electrons to enhance the degradability of recalcitrant biomass (Cannella et al., 2016; Villares et al., 2017). In nature, microbial degradation by oxidative and hydrolytic enzymes might provide plants with both endogenous and exogenous sources of carbon recycled from the host plant itself or from neighboring senescent plants. These in vitro studies show that microbes utilize oxidative processes to degrade wall polysaccharides, and further support the idea that oxidative ROS might a role in plant cell-wall autodegradation. Wall autodegradation has the potential to generate large amounts of accessible carbon for use by plant cells. Although the amount of carbon liberated from cell-wall autodegradation is largely unknown, uptake of degraded wall material hypothetically provides a method for plants to support growth without the metabolic investments required for de novo cell-wall biosynthesis.

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immunologically detected cell-wall polysaccharides in internal compartments, suggesting that large hemicellulose and pectin fragments might be endocytosed from the cell wall and incorporated into nascent cell plates in maize and wheat roots (Baluška et al., 2002, 2005; Yu et al., 2002). However, this conclusion was put into question by the finding that de novo secretory trafficking to the cell plate, and not endocytosis, is required for cytokinesis (Reichardt et al., 2007). Labeling and tracking experiments using additional cell-wall probes might help resolve questions concerning the endocytosis of large polysaccharide fragments from the apoplast. The uptake of wall-derived material is likely to consist mostly of the import of free monosaccharides or small oligo-saccharides, as there exists substantial evidence for uptake of apoplastic monosaccharides (Gibeaut and Carpta, 1991; Reiter et al., 1993; Burget and Reiter, 1999). The proton-coupled sugar transports, SUGAR TRANSPORT PROTEINS (STPs), of Arabidopsis are critical for exogenous sugar uptake in various tissues (Sherson et al., 2000). A recent study involving small cellulose-derived oligo-saccharides suggests that these molecules can be recycled (Souza et al., 2017): enhanced fresh mass accumulation of Arabidopsis seedlings grown on cellulose depended on β-glucosidase activity from AtBGLU27, indicating a metabolic boost from cellulosic oligosaccharide recycling (Souza et al., 2017). These findings relate to the common phenomenon in plants of enhanced root growth in the presence of exogenous sugars such as glucose and sucrose (Burström, 1948). Heterotrophic suspension-cultured plant cells, considered to be parenchymatous, can also acquire sugars and nutrients from an aqueous medium without roots. However, which transporters are required for the uptake of sugars derived from wall autodegradation, or how well different cell types are equipped to do so, is currently unknown.

After wall-derived sugars are internalized, they must be metabolically reactivated by salvage pathways into ND-P-sugars before serving as new substrates for wall polysaccharide biosynthesis (Figure 2C) (Bar-Peled and O’Neill, 2011). Different sugars have specific salvage pathways; for example, glucose is phosphorylated by HEXOKINASE (HXK) at the C6 position, PHOSPHOGLUCOMUTASE (PGM) isomerizes the phosphate group to the C1 position, and UDP-glucose pyrophosphorylase (UGP) finally generates UDP-glucose that can directly be used for glucan biosynthesis (2D) or NDP-sugar interconversion (Bar-Peled and O’Neill, 2011), whereas fucose can be converted to GDP-fucose by the bi-functional enzyme FUCOKINASE/GDP-FUCOSE PYROPHOSPHORYLASE (FKGP) (Katake et al., 2008). The canonical pathway for sugar salvage is monosaccharide phosphorylation at the C1 position, followed by nucleotide exchange through UDP- or GDP-pyrophosphorylase activity. Thus far, kinases have been identified for several monosaccharides, including galactose (Kaplan et al., 1997), arabinose (Sherson et al., 1999), fucose (Katake et al., 2008), galacturonic acid (Yang et al., 2009), and glucuronic acid (Pieslinger et al., 2010). Evidence from feeding experiments using radiolabeled xylose suggest that a pathway for xylose salvage also exists (Carpta et al., 1982), but this pathway has not yet been genetically or enzymatically elucidated.

Pyrophosphorylase enzymes bidirectionally exchange the phosphate group of sugar-1-phosphates with NTP to produce

METABOLIC RECYCLING OF APOPLASTIC CLEAVAGE PRODUCTS

Following degradation, wall-derived materials need to be imported into the cell before being metabolically recycled for cell-wall synthesis (Figure 2B). A limited number of studies

Please cite this article in press as: Barnes and Anderson, Release, Recycle, Rebuild: Cell-Wall Remodeling, Autodegradation, and Sugar Salvage for New Wall Biosynthesis during Plant Development, Molecular Plant (2017), http://dx.doi.org/10.1016/j.molp.2017.08.011

Molecular Plant •••, 1–16, ••• 2017 © The Author 2017.
NDP-sugar and pyrophosphate, thus completing the reactivation of salvaged sugars for use by cell-wall GTs. Although pyrophosphorylases often react with specific sugar-1-phosphates, a promiscuous UDP-sugar pyrophosphorylase (USP) capable of producing various UDP-sugars was identified in pea (Pisum sativum) (Kotake et al., 2004). Arabidopsis also encodes a USP, also referred to as SLOPPY (Geserick and Tenhaken, 2013b). AtUSP epistatically controls the activity of kinases important for sugar salvage, exemplified by downregulation of glucoronokinase in USP-miRNA knockdown Arabidopsis plants (Geserick and Tenhaken, 2013a). The targets of AtUSP include glucronic acid-1-P, galactose-1-P, galacturonic acid-1-P, xylose-1-P, and arabinose-1-P (Geserick and Tenhaken, 2013b). Knockdown of AtUSP leads to accumulation of cytoplasmic xylose and arabinose, concomitant with a decrease in cell-wall arabinose content (Geserick and Tenhaken, 2013b). Although arabinokinase and USP are thought to be important for an arabinose salvage pathway, accumulation of cytoplasmic xylose also indicates the existence of a salvage pathway for xylose, which provides further indirect evidence of a yet-to-be-discovered xylose kinase as previously discussed. Following metabolic reactivation of sugars, the resulting NDP-sugars can be used for hemicellulose and pectin biosynthesis (Figure 2E).

NEW TOOLS FOR STUDYING CELL-WALL RECYCLING

Recent advances in biochemical and microscopic tools and techniques provide new avenues to explore the physiological roles of cell-wall recycling through more targeted analyses of wall degradation and sugar salvage. Recently, a set of fluorescently labeled chitin oligosaccharide and oligogalacturionate probes was described with the intended purpose of labeling negatively charged, de-methyl-esterified HG (Mravec et al., 2014, 2017). Pulse-chase experiments with these probes or fluorescently tagged XGOs, coupled with confocal microscopy, might allow researchers to track the route of endocytosed hemicellulose or pectins in real time. Further development of dynamic, small-molecule probes for cell-wall epitopes is essential for full knowledge of the cellular mechanisms by which cell walls are recycled (Wallace and Anderson, 2012).

To draw conclusions about the relative contributions of de novo wall synthesis and recycling in the future, it is of critical importance to continue to study sugar salvage pathways in plants. Although the use of chemically modified sugar analogs has long been described in the literature to study sugar metabolism and cellular functions (Datema et al., 1980), there appears to be a resurgence in employing sugar analogs to study sugar salvage, particularly for cell-wall biosynthesis (Villalobos et al., 2015). Most of the described analogs are deoxy and fluorinated versions of monosaccharides found in plant cell walls. Villalobos et al. (2015) posit that deoxy analogs act as chain terminators during polysaccharide polymerization as the lack of a hydroxyl group would disable glycosidic bond formation, whereas fluorinated analogs inhibit GT activity by disrupting interactions of NDP-sugars with GT active sites (Villalobos et al., 2015). For example, 2-fluoro-fucose inhibits the incorporation of fucose into Arabidopsis cell walls (Dumont et al., 2015; Villalobos et al., 2015). NDP-sugar interconversion has also been investigated using fluorinated compounds as described in studies using synthesized UDP-2-fluoro-glucuronic acid to monitor the conversion and mechanism of UDP-apiose formation by UDP-o-apiose/UDP-o-xylose synthase (Choi et al., 2011; Eixelberger et al., 2017). In maize and pea etiolated seedlings, 2-deoxyglucose inhibits callose production during gravitropic responses (Jaffe and Leopold, 1984). Furthermore, a deoxy analog of 3-deoxy-o-manno-oct-2-ulosonic acid (Kdo), a sugar present only in RG-II, inhibits cytosolic CMP-Kdo synthase and, as a consequence, limits RG-II biosynthesis, resulting in severe root growth phenotypes similar to those reported for plants deficient in boron-mediated RG-II crosslinking (Smyth et al., 2013).

Click chemistry is an emerging tool for studying the incorporation of exogenously fed sugar analogs into plants. Click chemistry enables the detection of modified bio-orthogonal substrates destined for incorporation into complex molecules of interest, such as plant cell walls. The first report of click chemistry to study plant cell walls applied an alkynylated fucose analog to label wall matrix polymers (Anderson et al., 2012). Additional click chemistry probes for plant cell walls include analogs of glucose, which were found to associate specifically with root hair tips (McClosky et al., 2016), Kdo (Dumont et al., 2016), N-acetylglucosamine, which associates with glycoproteins (Hoogenboom et al., 2016; Zhu et al., 2016), N-acetylgalactosamine associated with glycoproteins (Hoogenboom et al., 2016), and several additional sugar analogs (Hoogenboom et al., 2016; Wang et al., 2016; Zhu and Chen, 2017), and even non-sugar components of walls such as monoglycosides destined for lignin incorporation in secondary cell walls (Bukowski et al., 2014; Tobimatsu et al., 2014; Pandey et al., 2015, 2016; Lion et al., 2017). These tools provide an alternative to tracking radio-labeled components and enable spatiotemporal resolution of cell-wall incorporation through confocal microscopy and Raman spectroscopy. Currently, intracellular detection of click components is limited by the toxicity of copper-catalyzed click reactions and the poor accessibility of fluorescent probes to intracellular compartments. Electron microscopy coupled with click labeling might provide a route to detect internalized wall components as previously described for the labeling of peptidoglycans in the bacterium Listeria monocytogenes (Ngo et al., 2016), although this technique has not been applied to plants. Further development of in vivo click chemistry (Hoogenboom et al., 2016) has the potential to allow for long-term tracking of cell-wall components during turnover, although the finding that not all sugar analogs incorporate efficiently into Arabidopsis roots (Zhu and Chen, 2017) suggests that click modifications can sometimes interfere with metabolic recycling.

Drugs have long been used as biological tools and are promising candidates for understanding the metabolic and physiological consequences of cell-wall recycling. Decker et al. (2017) recently reported the characterization of a collection of chemical inhibitors of UGP and USP activity, providing a unique opportunity to monitor the metabolic flux of NDP-sugars upon perturbation of both de novo NDP-sugar biosynthesis and salvage pathways (Decker et al., 2017). In addition to pharmacological and genetic perturbation of the enzymes involved in cell-wall autodegradation and metabolic recycling, purification and genetic manipulation of plant-derived inhibitory proteins, such as PMEIs, PGIPs, and XIPs, might provide new avenues to explore the physiological roles of cell-wall recycling through more targeted analyses of wall degradation and sugar salvage.
additional tools to investigate cell-wall recycling. A thorough understanding of sugar salvage on the metabolic level will also require refined biochemical analyses, such as those achieved with dynamic metabolic flux analysis (DMFA) of labeled sugars or wall material (Chen et al., 2013). Further efforts to discover drugs and sugar analogs will help to define the metabolic and physiological roles of cell-wall degradation, sugar salvage, and carbon recycling in plants.

Combining the aforementioned genetic and biochemical tools in heterotrophic plant culture systems, thereby avoiding the complexity of photosynthesis, provides a straightforward inroad to begin fleshing out the picture of cell-wall recycling. Maize coleoptiles were the system of choice for early studies of cell-wall recycling (Luttenegger and Nvins, 1985; Nock and Smith, 1987). Etiolated Arabidopsis seedlings have long been used in cell-wall research because their main metabolic activity is primary cell-wall biosynthesis, modification, and degradation to promote hypocotyl elongation (Peaucelle et al., 2015). Coupling the experimental tools, developmental characterization, and availability of numerous mutants and transgenic lines, Arabidopsis etiolated seedlings are a promising system with which to study wall autodegradation and sugar salvage (Minic and Jouanin, 2006; Xiao et al., 2014, 2017). Deconvolution of unknown aspects of cell-wall recycling such as metabolic flux, in muro degradation, and re-uptake pathways for sugars might be even easier to study in single-cell suspension cultures, which lack an epidermal cuticle. There is a current need for a robust and well-characterized suspension culture system representative of commelinoid monocots, providing a system complementary to tobacco BY-2 or Arabidopsis T78 cells. Optimization of a monocot suspension culture might be achievable by building from previously reported systems for rice (Amino and Tazawa, 1988), wheat and barley (Dong et al., 2010), switchgrass (Mazarei et al., 2011), and/or Spartina pectinata (Hogan, 1988). Advances in CRISPR-Cas9 technology and increasing genomic resources will bolster the number of facile genetic systems in the future. However, the complex genomic organization of grasses such as maize and wheat might require the utilization of other model grass species such as barley (Mascher et al., 2017) or Brachypodium distachyon (International Brachypodium Initiative, 2010; Gordon et al., 2014).

Our discussion up to this point has summarized evidence for wall recycling and applicable tools for studying how plants modify and degrade cell-wall polysaccharides, recapture freed sugars, and metabolically salvage those sugars. Given that plants appear to possess the capabilities to recycle most primary wall components, we now discuss several key physiological processes in which cell-wall recycling might have prominent importance.

**WHAT IS THE RELATIONSHIP BETWEEN WALL RECYCLING AND GROWTH?**

Of all the functions of plant cell walls, their role in determining growth patterns is one of the best established. As cell-wall biosynthesis is a large metabolic sink in plants, it makes intuitive sense for plants to reuse autodegraded primary wall materials to support new wall synthesis. An extreme case of this might occur during the construction of an entirely new cell wall during cytokinesis. Although doubt has been cast on the intracellular transport of larger wall components from parental walls to the cell plate (see above), it would be worthwhile to investigate the role of metabolic recycling of cell-wall-derived mono- or oligo-saccharides during cell division in the future.

Cell-wall degradation, cell division, and cell elongation are all required for seed germination and early seedling growth. Aside from the seed coat degradation that facilitates radicle emergence, several plant species degrade cell-wall components to support early seedling growth. Nasturtium (Tropaeolum majus L) seedlings mobilize apoplastic XyG reserves to fuel seedling growth and development (Edwards et al., 1988; Farutti et al., 1991; Crombie et al., 1998). Analogous to nasturtium seeds, Brachypodium distachyon seeds contain high levels of mannan in the coleorhiza and endosperm that are posited to contribute to two separate processes: preventing premature germination of the radicle and mobilizing endosperm-localized mannans (González-Calle et al., 2015). Degradation of arabinans during Arabidopsis seed germination also occurs (Gomez et al., 2009). Organ-specific microarray analysis of AtUSP and genes involved in sugar-1-phosphate formation depicts expression in all plant organs throughout the life cycle (Geserick and Tenhaken, 2013b). Furthermore, an increasing number of studies on pectin degradative genes demonstrate a critical role for pectin degradation in seedling elongation (Minic and Jouanin, 2006; Xiao et al., 2014, 2017). Together, these studies indicate the importance of cell-wall recycling in germination and early plant development.

Wall degradation is an important regulator of wall extensibility and cell elongation. Cell-wall recycling can help subsidize the construction of elongating walls. Wall-degrading enzymes function in elongating tissues such as stems and dark-grown hypocotyls (Xiao et al., 2014, 2017; Peaucelle et al., 2015). For example, elongating Arabidopsis stems exhibit relatively high expression of PL, XTH, β-1,3-xyllosidase, β-o-xyllosidase, α-L-arabinofuranosidase, β-o-glucuronidase, and β-D-mannosidase genes (Minic et al., 2009). Circumstantial evidence implies that the mechanisms by which plants grow might be tightly coupled with cell-wall recycling. The acid growth hypothesis states that upon acidification of the wall, cell walls become more extensible through expansin-mediated loosening (Cosgrove, 2005). Carpita et al. (1982) found that incorporation of exogenously supplied sugars into cell walls increased in maize coleoptiles upon auxin treatment, suggesting that auxin-induced acidification enhances sugar uptake (Carpita et al., 1982). Low concentrations of calcium also stimulated arabinose incorporation into maize coleoptile cell walls (Carpita et al., 1982), which might be connected to the degradation of calcium-complexed HG. Furthermore, some evidence supports the possibility of long-range transport of matrix polysaccharides through the vasculature in excised stems; these polysaccharides could be used to support new growth in elongating tissues (Baydoun and Fry, 1985; Warneck et al., 1998), but this type of transport has not been shown to occur in intact plants. Synthesis of these data indicates that cell elongation and sugar salvage resulting from cell-wall degradation are tightly correlated processes, but whether one drives the other remains to be determined.

One of the most tantalizing questions remaining to be answered about wall recycling is: what is the breadth of cell-wall recycling?
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across plant development? It is possible that all cells participate in recycling to at least a limited extent, as wall biosynthesis or degradation is associated with cell division, cell elongation, meristem maintenance and organ emergence, germination, plasmodesmata formation, and abscission. Sink tissues are excellent candidates for studying cell-wall recycling due to their heterotrophic nature. As previously discussed, etiolated seedlings have many advantages due to their anatomical simplicity and ease of use for live-cell imaging experiments. However, roots are likely the best example of a prominent plant organ in which one would expect high amounts of recycling due to their roles as sink tissues and their physiological function of scavenging nutrients and carbon from their environment. A dramatic example of how roots might utilize wall recycling during growth is aerenchyma formation in monocot roots. Aerenchyma are large porous regions of monocot roots that form in response to anoxic stress and ROS signaling to reduce the metabolic cost of maintaining older root segments and promote soil exploration by dedicating resources to new growth (Lynch, 2013; Xu et al., 2013). A recently discovered NADPH oxidase was found to be involved in large-scale cell-wall degradation during aerenchyma formation under anoxic conditions in rice roots, resulting from downstream effects of ethylene signaling (Yamauchi et al., 2017). Despite the established role of ROS in signaling, it is possible that oxidative bursts in roots might also trigger wall deconstruction. Aerenchyma formation is difficult to study in real time due to its anatomical position in internal root tissues, but the process undoubtedly requires massive wall deconstruction events that leave cell-wall remnants within the plant body. In terms of cell-wall recycling, aerenchyma formation and abscission zones represent valuable sources of wall-derived carbon and could be used as model systems to understand the metabolic fates of degraded wall materials.

Establishing connections between cell-wall recycling and cell elongation in plants is a difficult feat because of the poorly understood roles of both wall synthesis and wall degradation in controlling wall loosening and cell elongation (Cosgrove, 2016). In addition, it is not clear whether the rate of cell-wall biosynthesis correlates with rates of recycling, but investigation of these processes in parallel across species and tissues will provide insights into which developmental processes are most dependent on wall recycling. Studies describing the decoupling of seedling growth from cell-wall synthesis have provided insights into how seedlings regulate growth (Refregier et al., 2004; Derbyshire et al., 2007). If cell-wall biosynthesis and degradation can be experimentally decoupled in elongating tissues, this might provide a unique opportunity to explore the contributions of cell-wall recycling on plant growth. Uncovering links between cell-wall recycling and its impact on plant growth can help to enhance nutrient acquisition, biomass accumulation, and establishment of early growth in the life cycle of economically important crops.

HOW IMPORTANT IS WALL RECYCLING FOR REPRODUCTION?

During reproduction, numerous wall degradation events are required to facilitate floral development, organ separation, pollen formation, and anther dehiscence (Liljegren, 2012). Inflorescences also act as prominent metabolic sinks, thus building a case for why cell-wall recycling might conserve carbon resources during plant reproduction.

Although this hypothesis has not been directly tested, some of the most convincing evidence for a prominent role of cell-wall recycling during reproduction comes from gene expression and mechanical data investigating changes to cell walls in meristem tissues of Arabidopsis. Expression of FKG P is highest in floral buds (Kotake et al., 2008), ARA1 is highly expressed in flowers and anthers in particular according to the eFP Browser (Waese and Provart, 2016), and USP is highly expressed in flowers and is required for anther development and pollen viability (Geserick and Tenhaken, 2013b). Interestingly, the promiscuous activity of AtUSP points toward an enzymatic preference for the salvage of sugars highly abundant in pectin such as galacturonic acid, galactose, and arabinose (Geserick and Tenhaken, 2013b). Previous work detailing the mechanical contributions of pectins to bud maintenance and breaking in Arabidopsis implies that, in addition to the known roles of PME (Peaucelle et al., 2011), PGs and PLs likely weaken the walls of meristem cells through pectin degradation to allow for bud breakage and floral development. Furthermore, wall autodegradation during floral organ separation and abscission likely provides an abundance of salvageable pectin fragments and monosaccharides that can contribute to floral organ development (Rhee and Somerville, 1998; Rhee et al., 2003; Palusa et al., 2007; Cao, 2012; Xiao et al., 2014). Flowering and stem elongation are coupled processes in annual plants like Arabidopsis, so it is possible that wall recycling eases the metabolic burden of both processes, but it would be interesting to study the fate of degraded cell-wall materials in perennial plants that often undergo sexual maturation after years of development to assess whether sugar salvage for reproductive organ development takes metabolic precedence over salvage for elongation.

For angiosperms to reproduce, pollen must land on a receptive stigma, and a pollen tube harboring sperm cells must grow through the flower style to fertilize an ovule to produce an embryo. Pollen tubes grow at their distal tip by depositing cell-wall material and continually modifying that material to promote elongation, a different fashion of growth from that of most diffusely growing plant organs such as roots and stems (Chelbi et al., 2012). Pollen tubes are metabolically dependent on sugar salvage to fuel tip elongation, taking up sugars from stigmas and styles as they grow toward the ovule (Nøgaard, 1977). Transmission electron microscopy and immunofluorescence microscopy data suggest that cellulosic materials might be actively recycled in Arabidopsis pollen tubes during growth (Chelbi et al., 2012). Arabidopsis STP1, STP2, and STP10 proton-coupled sugar transporters are expressed in flowers. AtSTP2 expression is closely correlated with callose and tapetal cell degradation during microspore development, indicating a role for AtSTP2 in cell-wall recycling (Truenit et al., 1999). Furthermore, AtSTP10 is expressed in pollen tubes in response to low glucose levels (Rottmann et al., 2016). In addition to the previously discussed ubiquitous expression of AtUSP and sugar-1-kinase genes (Geserick and Tenhaken, 2013b), expression profiling of Lilium and Arabidopsis glucuronokinases revealed ubiquitous expression with highest expression in...
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pollen tubes, indicating the importance of sugar salvage or the MIOX pathway of UDP-glucuronic acid synthesis during pollen tube growth (Pieslinger et al., 2010). Notably, a class of drugs recently found to inhibit UGP and USP activity also inhibits pollen tube elongation (Decker et al., 2017). Considering the abundance of pectin-degrading activity in flowers and the well-established role of pectin in regulating tip growth in pollen tubes (Rhee and Somerville, 1998; Rhee et al., 2003; Palusa et al., 2007; Cao, 2012; Chebli et al., 2012), it is likely that degradation and recycling of pectin provides substrates for pollen tube growth (Geserick and Tenhaken, 2013b). Exploring the ways in which plants utilize autodegraded wall material for reproduction can provide novel strategies for enhancing plant production and fertility.

WHAT IS THE ROLE OF WALL RECYCLING IN SECONDARY CELL-WALL BIOSYNTHESIS?

Thus far, the developmental processes discussed in terms of cell-wall recycling have involved tissues undergoing growth, and therefore relate to recycling for the production of primary cell walls. However, secondary cell walls constitute the vast majority of biomass in plants and are a far more metabolically demanding carbon sink. In cell types that undergo secondary thickening, growth has completely ceased and there is no physiological need for primary wall synthesis. For these reasons, primary wall autodegradation might serve as a mechanism to fuel secondary wall formation, especially during the early stages of secondary thickening.

In cell types such as phloem fibers and xylem vessels, secondary cell walls fortify tissues and provide mechanical support. Secondary cell walls are composed of cellulose, decorated xylo-, and lignin, a polyphenolic polymer that crosslinks with polysaccharides and hydroxyxylanic residues found on xylans (d’Errico et al., 2015; Du et al., 2013; Vogel, 2008). Secondary walls are usually orders of magnitude thicker than primary cell walls, and thus require much more metabolic investment that primary walls for synthesis (Haigler et al., 2001). Elongating cotton fibers have been used as a model system for studying secondary wall biosynthesis and have provided insights into the processes controlling secondary thickening in plants (Gou et al., 2007). However, cotton fibers are unique in that secondary thickening mostly consists of cellulose biosynthesis without hemicellulose or lignin production, which is problematic when trying to draw general conclusions on secondary cell-wall biosynthesis across the plant kingdom. At the onset of secondary wall formation in vascular tissues, cells undergo large metabolic and transcriptional changes (Ohtani et al., 2016; Li et al., 2016a, 2016b). During the early stages of secondary wall formation in eudicots, glucuronoxylan and cellulose synthesis occur at high rates, which gradually decline as lignification begins. In tobacco BY-2 suspension culture cells expressing an inducible VND7 transcription factor that promotes secondary wall thickening characteristic of transdifferentiating xylem vessels, down-regulation of the biosynthesis of intermediates of glycosylation and transcriptional changes indicate increased flux toward glucogenesis, presumably for sugar production for cell-wall synthesis (Ohtani et al., 2016). Interestingly, a significant upregulation of genes involved in cell-wall degradation occurs in Arabidopsis seedlings undergoing VND7-induced transdifferentiation (Li et al., 2016b), similar to previous observations from hormonally induced transdifferentiating Zinnia elegans mesophyll cells (Ohdaira et al., 2002). DMFA, pulse-chase, and live-cell imaging experiments in inducible VND systems, as well as potentially in more complex systems such as developing stems, represent valuable tools for monitoring the fate of primary wall components during the transition to secondary wall biosynthesis.

Following secondary cell-wall polysaccharide synthesis, lignification initiates as cells start to undergo programmed cell death. Lignification is first evident at cell corners (Saka et al., 1982), which contain high levels of pectins in primary cell walls (Willats et al., 2001). Lignification might therefore involve pectin degradation, which might provide the cell with salvageable sugars before cell death occurs, although this hypothesis has not yet been tested. A poplar secondary wall master switch, SND1, genetically interacts with several pectin modifying and degrading enzymes as determined by chromatin immunoprecipitation experiments, showing direct co-regulation of secondary wall formation and pectin degradation (Lin et al., 2013). Recently, we reported that activation tag-induced overexpression of a polygalacturonase gene, POLYGLACTURONASE INVOLVED IN EXPANSION2 (PGX2), resulted in premature stem bolting and enhanced lignification in Arabidopsis. PGX2AT activation tagged plants might serve as a valuable model in which to study how excessive pectin degradation in stems leads to enhanced secondary wall synthesis (Xiao et al., 2017). After cell death, lignification continues through the supply of monolignols by neighboring parenchyma cells that do not undergo lignification (Hosokawa et al., 2001; Tokunaga et al., 2005; Pesquet et al., 2013; Smith et al., 2013). This “good neighbor” model essentially describes vessel lignification as both a cell-autonomous and non-autonomous process, although this is not currently thought to occur in all lignifying cell types (Smith et al., 2013). Stretching the “good neighbor” model to polysaccharide synthesis opens the possibility that sugars or wall fragments from neighboring cells or shared junctions such as middle lamellae contribute to the early stages of secondary wall formation, fueling xylan and cellulose biosynthesis. Given the presence of transxylanases in plants, the small amounts of primary wall xylans in eudicots might also be donated to neighboring cells undergoing secondary thickening, depending on how far xylan fragments can migrate. Degradation of XyG and pectin might also contribute glucose, xylose, arabinose, and glucuronic acid to secondary wall cellulose and xylan biosynthesis. Minic et al. (2009) described high expression levels of many predicted apoplastic proteases and hypothesized potential roles for these proteases in stem elongation, presumably by degrading structural wall proteins (Minic et al., 2009). The degradation of cell-wall proteins, such as AGPs, and uptake of aromatic amino acids from neighboring cells might also feed monolignol biosynthesis (Vanholme et al., 2010). Further explorations and tests of these hypotheses are necessary. Understanding the various sources of carbon used for secondary cell-wall biosynthesis can lead to the optimization of plant growth and biomass accumulation.
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FUTURE PERSPECTIVES

Cell-wall degradation is as vital to plant growth and development as cell-wall synthesis. However, cell-wall degradation has often been conceptualized as an end point of cell-wall dynamics despite early studies describing the capabilities of plant cells to recycle degraded wall material for sustainable development. As more genetic, chemical, metabolomic, and microscopy tools are developed, the contributions of cell-wall recycling to plant growth should become more apparent. Combining emerging approaches with traditional biochemical tracing and DMFA experiments to track the journey of cell-wall materials seems like an especially promising strategy. Understanding the physiological roles of cell-wall recycling would provide a deeper understanding of cell-wall dynamics and carbon flux during growth and developmental transitions and inspire new strategies for the optimization of biomass accumulation and cell-wall synthesis for production of food, cell-wall-derived biomaterials, and bioenergy.

FUNDING
This work was supported as part of The Center for Lignocellulose Structure and Formation, an Energy Frontier Research Center funded by the U.S. Department of Energy, Office of Science, Basic Energy Sciences under awardno DE-SC0001090.

AUTHOR CONTRIBUTIONS
W.J.B. and C.T.A. wrote and revised the manuscript.

ACKNOWLEDGMENTS
No conflict of interest declared. We thank members of the Center for Lignocellulose Structure and Formation and the Anderson Lab for helpful discussions.

Received: June 28, 2017
Revised: August 16, 2017
Accepted: August 21, 2017
Published: August 29, 2017

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Please cite this article in press as: Barnes and Anderson, Release, Recycle, Rebuild: Cell-Wall Remodeling, Autodegradation, and Sugar Salvage for New Wall Biosynthesis during Plant Development, Molecular Plant (2017), http://dx.doi.org/10.1016/j.molp.2017.08.011.
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Molecular Plant


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