

Review

Pectate lyases: Their role in plants and importance in fruit ripening

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ABSTRACT

Plant cell walls are complex structures that are modified throughout development. They are a major contributor to the properties of plant structure and act as barriers against pathogens. The primary cell walls of plants are composed of polysaccharides and proteins. The polysaccharide fraction is divided into components cellulose, hemicelluloses and pectin, are all modified during fruit ripening. Pectin plays an important role in intercellular adhesion and controlling the porosity of the wall. A large number of pectin degrading enzymes have been characterised from plants and they are involved in numerous aspects of plant development. The role of pectate lyases in plant development has received little attention, probably because they are normally associated with the action of plant pathogenic organisms. However their importance in plant development and ripening is now becoming well established and new information about the role of pectate lyases in plant development forms the focus of this review.

1. Introduction

The plant cell wall is a complex composite of polysaccharides and proteins. Around 90% of the wall is composed of polysaccharides and these fall into three broad classes, cellulose, hemicellulose and pectins. Recent models of the plant cell wall can be described as long, thin, strong, stiff groups of cellulose microfibrils, with hemicelluloses likely to be bound to some of these cellulose microfibrils and pectins filling the spaces between microfibrils (Cosgrove, 2018). The pectins are some of the most structurally complex polysaccharides. They are polymers of galactosyluronic acid with a range of other sugar residues involved in the polysaccharide backbone or acting as side chains. The principal forms of pectins in the cell wall that are currently recognised are homogalacturonan (HG), rhamnogalacturonan-I (RG-I), and rhamnogalacturonan-II (RG-II). HG is composed of long stretches of galactosyluronic acid residues some of which can be methylesterified. RG-I is composed of a backbone of alternating galactosyl and rhamnosyl residues, with some of the rhamnosyl residues harbouring sidechains of galactosyl or arabinosyl residues. RG-II is a more complex polysaccharide with residues that include galacturonic acid rhamnose, galactose, apiose and aceric acid (O'Neill, Ishii, Albersheim, & Darvill, 2004). Pectins play important roles in the cell wall structure (Cosgrove, 2018). The middle lamella and tricellular junctions between cells are

rich in pectins and these molecules play an important role in cell-to-cell adhesion (Daher & Braybrook, 2015).

The cell wall provides a barrier to pathogen infection. Pathogenic organisms penetrate plant tissues through wounds or the cuticle. They then secrete large amounts of pectin degrading enzymes into the intercellular spaces (Barras, Gijsegem, & Chatterjee, 1994; Collmer & Keen, 1986) and pectin degradation results in dissolution of the middle lamella. This can occur in almost all plant tissues including leaves, stem, fruit, tuber or roots, causing tissue damage, cell rupture and complete maceration of tissues within a few days.

Pectate lyases (PLs) are major pectin degrading activities produced by pathogenic organisms. PLs and other cell wall degrading enzymes can act as virulence factors, which enhance the potential to cause disease and play an essential role in infection process. PLs are, alkaline pectinases, that are also known as pectate transeliminases. They randomly cleave $\beta(1-4)$ linkages between galacturonosyl residues by β -elimination generating 4,5-unsaturated double bonds oligogalacturonates (Marín-Rodríguez, Orchard, & Seymour, 2002; Abbott, Gilbert, & Boraston, 2010). PLs can also macerate and disassemble the plant cell wall and tissues in a manner similar to that occurring in fungal diseases (Collmer & Keen, 1986). The main substrate for PLs is thought to be homogalacturonan (HG) which consists of a α -1,4 linked galacturonic acid (GalpA) units. The pH for reactions catalysed by these enzymes in

Abbreviations: CWDEs, cell wall degrading enzymes; HG, homogalacturonan; PG, polygalacturonase; PL, pectate lyase; PME, pectin methyl esterase; B-GAL, galactanase

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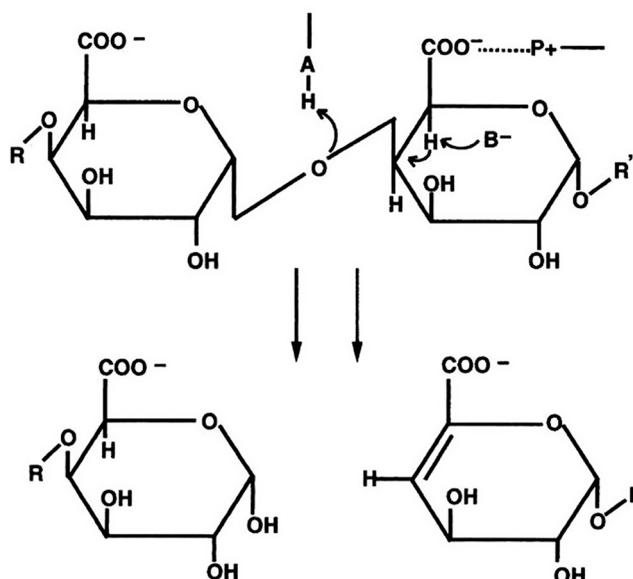


Fig. 1. Schematic diagram of α -1,4-polygalacturonic acid cleavage by a β -elimination mechanism. The pectate lyases are expected to contribute a minimum of three groups to the catalytic mechanism: P+, which neutralizes the charge on the carboxylic acid group; B, a general base that abstracts the proton from C-5; and A, which is involved in the transfer of the final proton to the glycosidic oxygen, leaving a double bond between C-4 and C-5 (from Herron, Benen, Scavetta, Visser, & Jurnak, 2000).

in vitro extends from 6 to 10 with an optimum near pH 9 for most isozymes. Also the reaction has a requirement for calcium ions (Tardy, Nasser, Robert-Baudouy, & Hugouvieux-Cotte-Pattat, 1997; Collmer, Reid & Mount, 1988) (Fig. 1).

PL activity was first discovered in cultures of *Erwinia carotovora* and *Bacillus* sp. (Starr & Moran, 1962). PL proteins have since been purified and characterized in microbial organisms (Dubey, Yadav, Kumar, & Anand, 2016). Measurement of PL activity in plant extracts has proved challenging (Besford & Hobson, 1972) and this probably explains why it took until the advent of molecular biology techniques and the detection of PL transcripts, for the potential importance of endogenous plant encoding PL genes to become apparent. Indeed, genes encoding PLs are expressed at almost all stages of plant development in a wide range of plant species (Wang, Yeats, Uluisik, Rose & Seymour, 2018), however their role in plant development is still poorly understood. This review focuses on recent reports of PL gene expression and enzyme action in plants and explores the possible role of these enzymes in cell wall remodelling during a range of plant developmental processes.

2. PL and plant pathogens

PLs have been most extensively studied in *Erwinia chrysanthemi* which is a member of the soft-rot enterobacteriaceae family. These bacteria cause severe damage on numerous economically important crops including potato with yield reductions of 20–25%. (Toth et al., 2011; Motyka, Zoledowska, Sledz, & Lojkowska, 2017). These enzymes are now known to be important for a wide range of plant pathogenic microorganisms. For example, *Xanthomonas gardneri*, causes water-soaked disease lesions on fruits and leaves during bacterial spot of tomato. The activation of PL gene expression resulting in increased hygroscopicity of the cell wall which may reflect the increased tissue maceration from PL activity (Schwartz, Morbitzer, Lahaye & Staskawicz, 2017). Cho et al. (2015) identified a PL1332 gene in *Alternaria brassicicola* which causes black spot disease on the leaves and stems of *Brassica* species. Strains where the PL1332 gene was deleted were approximately 30% less virulent than wild-type *A. brassicicola*

(Fig. 2). This study indicated that PL encoded by PL1332 toxin-encoding gene was highly expressed during the early infection process. In a similar study, *Nicotiana benthamiana* was infected by *Verticillium dahliae*, which is a wide-host-range pathogen that secretes a large number of cell wall degrading enzymes, including 13 PLs. The expression of *VDPEL1* was most significantly up-regulated during the infection stage (1.5–3 days). The study claimed that early expression of *VDPEL1* may help the pathogen to extract nutrition (Yang et al., 2018). Important pathogens of fruit crops that show high levels of PL activity or gene expression are shown in Table 1.

The mode of action of fungal PLs has been studied in detail. The crystal structure of PLs of *Bacillus* sp. (Zheng et al., 2012) and *Erwinia chrysanthemi* (Creze et al., 2008) have been reported and 3D structures of 28 polysaccharide lyases representing different species of *Aspergillus* were predicted using homology modeling (Kumar, Yadav, Nasim, & Yadav, 2014). On the basis of amino acid sequences, PLs belong to the larger class of polysaccharide lyases and occur in 5 (PL1, PL2, PL3, PL9 and PL10) of the current 28 of polysaccharide lyase families (<http://www.cazy.org/Polysaccharide-Lyases.html>). Several different protein folds have been observed among PL enzymes in which the main protein architectures PL2 and PL10 are (a/a)_n barrel folds, in contrast PL1, PL3 and PL9 adopt parallel beta-helix folds. These parallel beta-helix folds are similar to fungal pectin lyases A and B, pectin methylesterase (PME), polygalacturonase (PG), and rhamnogalacturonase. Although the members of these family enzymes (PL1, PL3 and PL9) do not share sequence homology, their structural similarities suggest that they had a common ancestor. The general β -elimination mechanism used by all PLs is similar. It involves a basic residues, Arginine (PL1, PL2, and PL10), Lysine (PL3 and PL9) or Histidine (PL22). The catalytic mechanism requires a basic residue (usually an arginine) to abstract the α -proton at position C5 atom of the substrate (galacturonate residue) which has been acidified by the Ca^{+2} ions at the active site (Hugouvieux-Cotte-Pattat, Condemine, & Shevchik, 2014).

3. Plant PLs

The first PL-like genes were identified from anthers and pollen. Identification of two genes *LATE ANTHET TOMATO 56* (LAT 56) and *LATE ANTHET TOMATO 59* (LAT 59) that were abundantly expressed in mature anther and pollen in tomato and with strong sequence similarity to *Erwinia* PLs led to the first identification of Pectate lyase-like (PLL) gene sequences in plants (Wing, Yamaguchi, Larabell, Ursin, & McCormick, 1989; Turcich, Hamilton, & Mascarenhas, 1993). A peptide fragment with significant homology to PL isozymes was reported from Japanese cedar (*Cryptomeria japonica*) pollen and Cryj I, a major allergen of Japanese cedar pollen, was shown to react with polygalacturonic acid, resulting in the release of unsaturated uronide products (Taniguchi et al., 1995). Another early successes in determining PL activity from plant tissues included work published by Domingo et al. (1998) who demonstrated activity in elongating and differentiating *Zinnia* (*Zinnia elegans*) cell cultures.

PLL genes have now been reported from a wide range of species including alfalfa (Wu, Qiu, Du, & Erickson, 1996). *Arabidopsis* (Sun, & van nocker, 2010), *Brassica rapa* (Jiang, Yao, Miao, & Cao, 2013), cotton (Wang et al., 2010), poplar (Bai et al., 2017), rice (Zheng et al., 2018) and tobacco (Rogers, Harvey, & Lonsdale, 1992). In *Arabidopsis* 26 genes have been annotated as PLL (Palusa, Golovkin, Shin, Richardson, & Reddy, 2007). The expression of these genes is associated with a diverse range of processes and organs including pollen development, flowers, roots, leaves and stems. All 26 genes are expressed in flowers. Fourteen PLL genes were specifically expressed in the pollen and pistils (Palusa et al. (2007).

Chinese cabbage (*Brassica campestris*) has been used to characterize the PLL gene function in pollen development (Jiang et al., 2014). In this study, antisense-RNA lines of *BcPLL9* (*bcpll9*) produced shorter length pollen tubes with an uneven surface. The authors concluded that

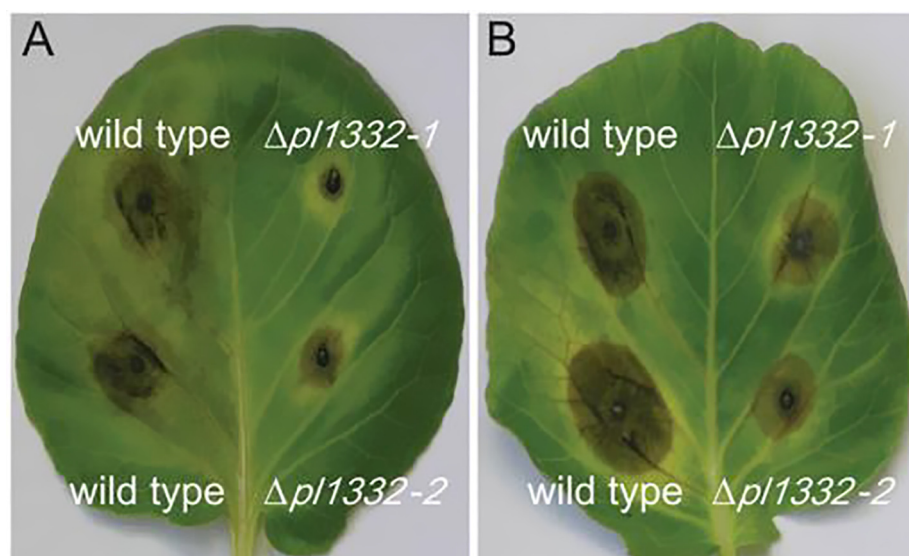


Fig. 2. Lesions caused by two strains of $\Delta p1332$ mutants and wild-type *Alternaria brassicicola* on leaves of green cabbage, *Brassica oleracea*. Pictures were taken 5 days post-inoculation. (A) Assay results on a detached leaf, (B) Assay results on leaves attached to plants (leaves detached for photographing) (Cho et al., 2015). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Characterization of *PL* genes from plant pathogens and induction of *PL* genes in host.

Pathogen	PL characterization	Reference
<i>Heterodera glycines</i> (nematode)	Genes that encode PLs were cloned and characterized from the soybean cyst nematode, <i>Heterodera glycines</i> . Two types of PL are present in the nematode genome and likely have different roles during infection.	Peng et al., 2016
<i>Phytophthora capsici</i> (pathogen)	Cloning of <i>PL</i> genes from a highly aggressive strain of <i>Phytophthora capsici</i> 12 <i>PcPL</i> genes highly induced during infection of pepper and tobacco	Fu et al., 2015
<i>Verticillium dahliae</i> (fungal pathogen)	In search of <i>V. dahliae</i> Vd991 cell death-inducing proteins, a PL was identified (VdPEL1) that exhibited pectin hydrolytic activity, which could induce strong cell death in several plant species	Yang et al., 2018
<i>Xanthomonas citri</i> (canker bacterium)	Bacterial canker is caused by <i>Xanthomonas citri</i> subsp. <i>citri</i> (Xcc). Pel3 of Xcc strain XW19 is demonstrated as a virulence factor.	Chieh Chang, Deng, Huang, Chung, & Tzeng, 2016
<i>Debaryomyces nepalensis</i> (yeast strain)	Isolation of a yeast strain from apple producing PL	Sathyanarayana & Kumar, 2006
<i>Erysiphe cichoracearum</i> (powdery mildew on <i>Arabidopsis</i>)	PMR6 encodes a PL-L protein with a novel C-terminal domain. When gene mutated plants resistant to powdery mildew.	Vogel, Raab, Schiff, & Somerville, 2002
<i>Pectobacterium carotovorum</i> (soft rot of calla lily, <i>Zantedeschia</i> spp.)	PL activity related to soft rot disease. Temperature effect on PL activity tallied with that on tuber maceration.	Ni, Guo, & Custers, 2010
<i>Meloidogyne incognita</i> (Root-knot nematode)	Altered expression of a <i>PL</i> on nematode infection	Guan et al., 2017

BcPLL9 was probably associated with pectin metabolism during intine formation and had a function in pollen development and germination. In another study down-regulation of the *Brassica campestris PLL-10* gene resulted in low seed number, again consistent with a role for PL in pollen development (Jiang et al., 2014; Ju Rhee, Seo, Jeong, Cho, & Lee, 2015). Recently it has been shown that during pollen tube elongation in *Arabidopsis*, PLs are required for intine loosening during pollen germination and after this process PLs also make a contribution to the digestion and loosening of the pollen tube path during pollen elongation (Chebli & Geitmann, 2018).

A large number of putative *PL* encoding genes have been identified in the genomes of three cotton (*Gossypium*) species (Sun et al., 2018) with 53, 42 and 83 putative *PLL* genes being identified in *Gossypium raimondii*, *Gossypium arboreum* and *Gossypium hirsutum*, respectively. Transcriptomic data analysis showed that majority of these genes were expressed in stamens, during pollen development and fiber elongation stage. Cotton fiber elongation is known as an important stage during fiber development and the process is mainly achieved by cell wall loosening. PL activity increased rapidly at the fiber elongation stage and was coincident with depolymerisation of de-esterified pectin for fiber wall loosening (Wang et al., 2010). In the same study, when a *PL* gene was silenced in antisense lines, the PL enzyme activity decreased and a shorted-fiber phenotype was observed. This work indicated that PLs are important in cotton fiber cell wall loosening and fiber elongation.

PLs have been implicated in secondary wall formation. In Poplar (*Populus trichocarpa*) many genes encoding pectin-related enzymes such as PMEs, PGs and PLs are highly expressed in the transition between primary and secondary wall formation, which may be related to the digestion of the pectin-rich layer of the primary wall (Mellerowicz & Sundberg, 2008). Plant growth and xylem development was reduced by overexpression of *PtPL1-18* resulting in transgenic poplar trees with reduced secondary cell wall thickening and irregular xylem cells probably due to their lower pectin content (Bai et al., 2017). Overexpression of a *PLL* gene (*PtxtPL1-27*) which was expressed in differentiating xylem at the onset of secondary wall formation in hybrid aspen (*Populus tremula* L. × *tremuloides* Michx.; Ptxt), was found to increase the solubility of not only pectins, but also xylans and other hemicelluloses (Biswal et al., 2014). These results indicate that *PL* genes are important in pectin modification and secondary wall formation of woody plants.

PLL genes have been shown to have a role in leaf growth and senescence in rice (Leng et al., 2017). Mutation of the *DEL1* gene, which was predicted to encode a PL precursor, led to a phenotype involving abnormal plant growth and leaf senescence. Down-regulation of *DEL1* decreased PL activity, increased the degree of methylesterified HG, and perturbed cell wall composition and structure. Additionally two *PLL* genes in rice (*OSPSE1*, *DEL1*) were investigated by mutant analysis and shown to be involved in leaf senescence (Wu, Wang, Chen, Liu, & Chen, 2013; Leng et al., 2017).

Abscission-related processes have been linked to *PL* gene expression. Fruit peeling can be classified as a process where an abscission zone develops, but a force is required to separate the peel from the flesh. In a study carried out by Prakash et al. (2017) on kiwifruit (*Actinidia melanandra*) the *PL1* gene, described in (Atkinson et al., 2011), had a higher level of expression in good peeling kiwi genotypes than in those where peeling was more difficult. Genes that are highly up-regulated in stamen abscission zones include *PL*, pectin acetyltransferase, polygalacturonase, pectin methylesterase and expansins (Lashbrook & Cai, 2008). In rose (*Rosa bourboniana*), *RbPEL1* gene expression increased with the abscission process, being fastest during ethylene-induced abscission (Singh, Tripathi, Nath, & Sane, 2011). In a more recent study *PL* gene expression was observed in rose petal abscission and linked to regulation by ethylene. Gao et al. (2019), reported that two APETALA2/Ethylene-Responsive Factor (AP2/ERF) transcription factor family members were involved in regulating many genes related to pectin-metabolizing enzymes. Their data indicate that ethylene repressed *RhERF1* and auxin induced act together as a module, integrating ethylene and auxin signals to regulate the abscission process. The role of plant hormones in the control of processes such as abscission is well known, with ethylene acting to promote the process and auxin as an inhibitor, but the data from rose provide a link between hormone signalling and cell wall remodelling.

4. PLs in ripening fruits

Fruit ripening is a complex developmental process that involves substantial changes in gene expression leading to alterations in flavor, aroma, colour and texture (Giovannoni, Nguyen, Ampofo, Zhong, & Fei, 2017). Modifications in texture result in firmness loss, short postharvest life and difficulties in transportation. Fruit softening is closely linked to cell wall remodelling and especially degradation of pectin and other cell wall polysaccharides (Brummel, 2006). Pectins are known as the major constituent of the primary cell wall and middle lamella of fruit pericarp. A diverse group of enzymes and non-enzymatic cell wall modifying proteins are involved in remodelling and degrading polysaccharides during fruit ripening. Some of these cell wall degrading enzymes are particularly well characterized such as polygalacturonase (PG) (Ke et al., 2018) which cleaves to the α -(1,4)-galacturonosyl linkages in unesterified pectin. Pectin methyl esterase (PME) removes the methyl groups from the methylesterified homogalacturonan HG. Galactanases (β -GAL) catalyze the hydrolysis of β -galactans. PG and β -GAL can be endo or exo acting enzymes (Wang, Yeats et al., 2018). Rhamnogalacturonate lyase (Posé et al., 2019) degrades the rhamnogalacturonan -I (RG-I) backbone. The Tomato Genome Consortium (2012) found that more than 50 cell wall structure-related genes were expressed during ripening in tomato (*Solanum lycopersicon*) and many of these genes encoded enzymes/proteins that could degrade pectin (summarised in Fig. 3).

PLs are known to play an important role in the softening of fleshy fruits and are key components of the cocktail of enzymes involved in ripening-related cell wall remodelling. The first experimental evidence for their role in fruit firmness was demonstrated by work on transgenic antisense *PL* lines in strawberry. Silencing a strawberry (*Fragaria* $\times$ *ananassa*, Duch., cv Chandler) *PL* gene resulted in fruits that were 30% firmer than the controls (Jiménez-Bermúdez et al., 2002). *PL* gene expression during fruit ripening has also been reported in banana, *Musa* AAA group (Dominguez-Puigjaner, Llop, Vendrell, & Prat, 1997; Marín-Rodríguez, Smith, Manning, Orchard, & Seymour, 2003) and grape (*Vitis vinifera* L.) (Nunan, Davies, Robinson, and Fincher (2001). More recently in tomato (*Solanum lycopersicum*), a *PL* gene has been shown to play an important role in fruit softening (Uluisik et al., 2016; Yang et al., 2017; Wang, Yeats et al., 2018; Wang, Samsulrizal et al., 2018). In strawberry and tomato the mechanism of *PL* action has been studied in some detail. The action of *PL* in strawberry seems to be against tightly bound pectins (Doménech et al., 2008). Histological

observation revealed smaller intercellular spaces and greater contact areas between adjacent cells in low *PL* transgenic strawberry fruits (Paniagua et al., 2017). In tomato, immunocytochemistry indicated *PL* targeted de-esterified pectins which were concentrated in the tricellular junction zones between cells and the middle lamella regions (Uluisik et al., 2016). Work on transgenic tomato *PL* lines has also indicated reduced susceptibility to grey mould (Yang et al., 2017). Therefore *PL* can be considered as playing roles in both ripening and pathogen resistance.

In mango (*Mangifera indica* var. *Dashehari*) *PL* enzyme activity was detected in optimum levels at pH 8.0 and with 0.5 mM Ca^{2+} . Transcript accumulation of *MiPEL1* increased strictly during ripening and ethylene application induced the expression of this gene. Another mango variety, Alphonso, which is known to have a long shelf life, showed slower induction of *PL* gene expression during fruit ripening compared to varieties Dashehari and Kent; in which also 4 *PL* encoding transcripts were up-regulated (Deshpande et al., 2017). In banana, two distinct cDNA clones showing sequence homology to higher-plant *PL* genes were isolated. The transcripts were detected only in fruit tissue and both were strongly ripening-related. Measurements of *PL* enzyme activity in banana revealed a significant increase in calcium-dependent activity during ripening (Marín-Rodríguez et al., 2003).

5. Conclusion

PLs are an important part of a cocktail of enzymes controlling cell wall remodelling in a wide range of plant developmental processes. Based on the evidence in the literature the specific role of PLs in cell separation processes and how they might interact with other cell-wall remodelling activities to bring about cell separation is beginning to become clear.

Solid-state NMR data indicate pectins are closely associated with cellulose (Phyo, Gu, & Hong, 2019) and changes in the structure of the pectin fraction are intimately linked with cell expansion. For example, auxin treatment results in cell expansion and the presence of auxin results in wall acidification and the expression of genes encoding pectin methylesterases and PLs in Arabidopsis roots (Laskowski, Biller, Stanley, Kajstura, & Prusty, 2006). Wall acidification neutralizes galacturonic acid residues and changes the structure and dynamics of the polysaccharide network. The pectins become partially separated from cellulose microfibrils (Phyo et al., 2019). The action of galactanase, polygalacturonase and PL then alters pectin structure and likely prevents them from returning to their original conformation and association with cellulose. Degradation would also restrict aggregation and the formation of calcium crosslinking. Studies undertaken by Posé et al. (2015) in strawberry where the pectins were extracted from transgenic strawberry lines with reduced PG or PL. When the soluble pectins were analysed in both PG and PL silenced lines they had higher molecular weights, showed more aggregation and were more branched. The authors hypothesised that PG and PL are needed to degrade homogalacturonan and also for RG-disassembly as reflected by the higher density of aggregates in transgenic samples. Very recently rhamnogalacturonate lyase has also been implicated in strawberry softening (Posé et al., 2019).

In pathogen infections PLs play roles as virulence factors. In *Colletotrichum gloeosporioides* produces PL (pelB) during colonization of infected avocado tissue and the PL disruption via homologous recombination reduced fungal virulence by approximately 40% (Yakoby, Freeman, Dinoor, Keen, & Prusky, 2001). This result showed that PLB is an important factor in the attack of *C. gloeosporioides* on avocado fruit, probably as a result of its virulence factor and role in the induction of host defense mechanisms. In *Colletotrichum coccodes*, *CcpelA* may be a key virulence factor with a point mutation in a PL gene determining the aggressiveness of the pathogen and secretion into the plants (Ben-Daniel, Bar-Zvi & Tsror Lahkim, 2012). Plant defense responses include pathogen recognition via damage-associated molecular patterns, such as

Gene Expression Levels of Pectin Related Genes

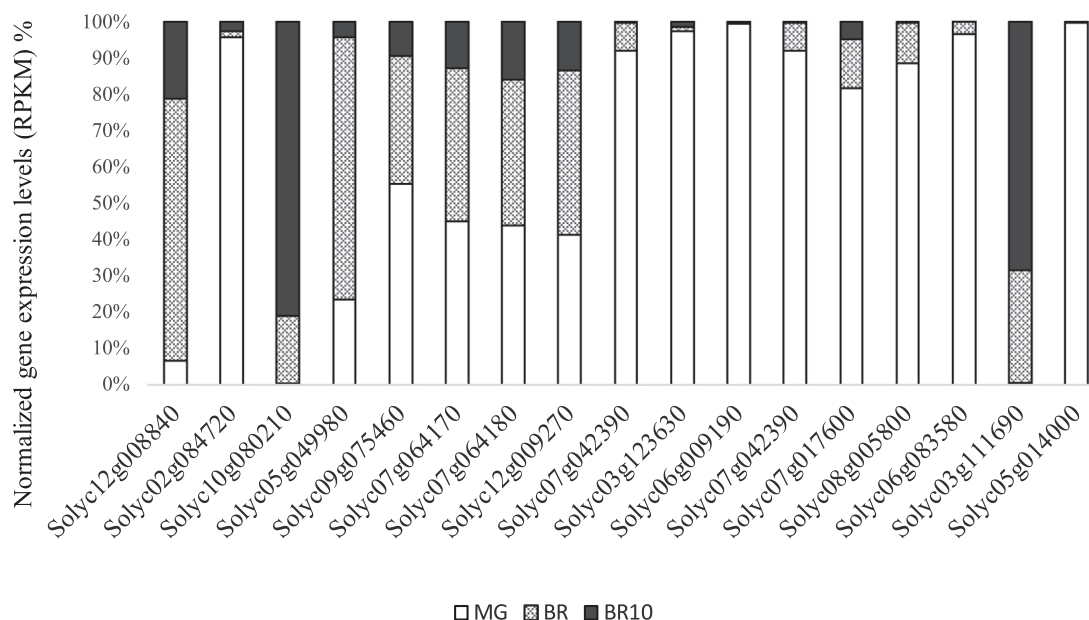


Fig. 3. Expression of pectin degrading enzymes in ripening tomato fruits based on RNASeq data (see [The Tomato Genome Consortium, 2012](#), supplementary Table 12). Ripening stages are shown as MG = mature green (white bars), BR = breaker/onset of first colour (textured bars), and BR10 = breaker + 10 red ripe (black bars). *BETA-GALACTOSIDASE*: Solyc12g008840 and Solyc02g084720; *POLYGALACTURONASE 2A*: Solyc10g080210; *POLYGALACTURONASE*: Solyc05g049980; *POLYGALACTURONASE-LIKE PROTEIN*: Solyc09g075460; *PECTINESTERASE*: Solyc07g064170, Solyc07g064180, Solyc12g009270, Solyc07g042390, Solyc03g123630, Solyc06g009190, Solyc07g042390, Solyc07g017600; *PECTINACETYLESTERASE*: Solyc08g005800; *PECTATE LYASE*: Solyc06g083580; Solyc03g111690 and Solyc05g014000.

fragments of plant cell wall released by the action of plant cell wall-degrading enzymes including PLs secreted by pathogenic microorganisms. This allows pathogens can be recognised by the plant immune systems through the action of pectic enzymes secreted by bacteria at the site of infection ([Expert et al., 2016](#)).

Outstanding questions for future research include the precise targets of PL action amongst the complex composite of cell wall polysaccharides and how PL action integrates with the activity of other cell wall degrading activities to drive cell wall remodelling during developmental processes.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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