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# More than cell wall hydrolysis: orchestration of cellular dynamics for organ separation Yuree Lee<sup>1,2</sup>



Plants' ability to cope with the ever-changing environment is one of the hallmarks that distinguishes plants from animals. Plants stationed in one place have evolved to remodel their architecture in response to the environmental factors by continuously creating new organ systems and removing existing organs through abscission. Herein, I provide insights into developmental plasticity of plants, focusing on the exit strategy (abscission). When plants start developing organs, the elimination tactics are also established in the form of abscission zones (AZ), that is, specialized cell layers for organ separation. Herein, recent advances in understanding the spatial regulatory mechanism of AZ in terms of cellular dynamics, coordination, and reconfiguration of the physical barrier of the cell wall to achieve precise abscission are discussed.

### Addresses

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# Introduction

Plant cells are surrounded by and attached to a rigid cellulosic extracellular matrix, the cell wall, which provides structural support to cells and tissues and plays an integral role in cellular processes, such as proliferation, differentiation, and defense [1,2]. Recent studies in floral organ abscission in *Arabidopsis* have provided insights into how the specific architecture is associated with cellular function and how local cell wall modification could be achieved [3<sup>••</sup>,4,5<sup>•</sup>]. Abscission occurs at a specific site, the abscission zone (AZ), which is generally established at the time of organ formation. When abscission is activated, the dissociation of the cell wall takes place in the AZ, resulting in organs' separation [6]. Moreover, abscission

has been adopted in the processes of flower fall and seed or fruit dispersal, making abscission an important aspect in human food supply and plant fitness [7–11]. This review focuses on the recent advances in mutual relationship between cellular function and architecture using organ abscission as a model system.

# Main text of review

### Coordination of layer-specific functions

Forward and reverse genetic screens using Arabidopsis have helped identify the signaling components of abscission including plant hormones ethylene and auxin, peptide ligand (IDA), receptor-like kinases HAESA (HAE) and HAESA-like 2 (HSL2), and mitogen-activated protein kinase cascades [12-16,17<sup>••</sup>], which were well summarized in recent reviews [18-20]. Compared to the well-identified signaling components that regulate abscission in a timely manner, our understanding of the cellular features and spatial regulatory mechanisms of abscission remain limited. How several layers of cells in AZ coordinate to dissolve middle lamellae and achieve subsequent organ separation, how the specificity of each layer is assigned, and how the cell wall remodeling is restricted to a specific area remains unelucidated. Recently, Lee et al. [3"] provided clues about layerspecific coordination of cellular dynamics and cell wall remodeling for precise abscission. In Arabidopsis, cell separation occurs between two adjacent cell layers, resulting in an even surface on the plant body after abscission. On the basis of the separating layer, AZ cells could be distinguished into cells that remain at the plant body after abscission and those that are attached to the shedding organ, which were defined as residuum cells (RECs) and secession cells (SECs), respectively [3<sup>••</sup>]. SECs and RECs behave differently, presenting cell-type-specific gene expression, ROS distribution, and cell wall modification (Figure 1). Molecular mechanisms for these layerspecific effects are not fully understood, but the research has pointed out the importance of spatial regulation in abscission and the necessity for investigating the layer specificity of the abscission process.

Lee *et al.* [3<sup>••</sup>] suggested that cell-type-specific ROS distribution plays an important role in maintaining specificity of abscission layers. The two neighboring cell types, RECs and SECs, show different accumulation patterns of ROS, high accumulation of superoxide  $(O_2^{-})$  and hydrogen peroxide  $(H_2O_2)$ , respectively. When this ROS pattern is disturbed in *nevershed (nev)* mutants, cell-type-specific activity is also affected [3<sup>••</sup>].





Illustrations of layer-specific cellular features and developmental transition of the abscission zone (AZ) in *Arabidopsis* flowers. (a) A drawing of the floral AZ in *Arabidopsis*. AZ cells attached at the 'cut surface' of the abscised flower (secession cells, SECs) are distinguished from AZ cells remaining at the receptacle (residuum cells, RECs) in terms of lignin formation and ROS distribution. H<sub>2</sub>O<sub>2</sub> preferentially accumulates at SECs, whereas superoxide accumulates at RECs. Lignin in SECs provides a physical barrier to confine the diffusion of cell wall enzymes, while the cuticle on the RECs protects the exposed surface.

(b) A schematic model for developmental transition of AZ cells in *Arabidopsis* flowers. Activated AZ cells present layer-specific cellular activities and architectures, though it is unknown as to when and how RECs and SECs are specified. Activated RECs undergo longitudinal expansion, which may contribute to reducing the rigidity of the xylem by inducing stretching and rupture of the lignified structure. After abscission, RECs become the outermost layer responsible for protecting against water loss and pathogen infection. Instead of forming protective layers associated with periderm, RECs of *Arabidopsis* flowers protect the surface by transdifferentiating themselves into epidermal cells and sealing the surface with cuticle.

In nev mutants, SEC-specific lignin is detected in RECs and the protective layer of REC is not formed. NEV is an ADP-ribosylation factor-GTPase-activating protein (ARF-GAP) that localizes at the trans-Golgi network and endosomes, and mutation in the gene influences membrane trafficking and inhibits floral organ abscission [14]. Transcriptomic analysis and measurement of the force needed to remove petals suggest that the underlying mechanisms of the abscission deficiency in *nev* are distinct from those of *ida* and *hae hsl2* mutants [21,22]. Interestingly, AZ cells of *nev* are ectopically enlarged, suggesting that cell wall loosening is not a factor that inhibits organ separation. Extensive cell expansion is observed in plants overexpressing IDA, wherein organ abscission is accelerated [23]. Disturbed cell-type-specificity in *nev* might be the answer to the puzzled phenotype of nev. Overaccumulation of H<sub>2</sub>O<sub>2</sub> at the RECs in *nev* may accelerate cell wall loosening and induction of defense-related gene expression, while inhibiting organ separation by ectopic lignin in RECs.

Different types of ROS play distinctive roles. Particularly, transition from proliferation to differentiation is controlled by balancing superoxide and  $H_2O_2$  accumulation in both plant and mammalian systems [24,25]. In roots, the consumption of  $H_2O_2$  by peroxidases, regulated by the transcription factor UPBEAT1, has been suggested to be important in maintaining the balance between superoxide and  $H_2O_2$  [24]. In AZ,  $H_2O_2$  concentration in SECs is strongly affected by the inhibition of superoxide dismutase (SOD) activity [3<sup>••</sup>] suggesting that the enzymatic conversion of superoxide into  $H_2O_2$  is another regulatory point for maintaining ROS balance. Further characterization of peroxidases and SODs would help clarify the different roles of superoxide and  $H_2O_2$  and to understand the molecular mechanisms by which cells maintain the specific balance between these ROS.

### Spatial distribution of lignin in abscission

Lignification in and near the AZ has been noted from the earliest study [26] and it has been suggested to play a role

in protecting the area exposed after abscission [27,28]. However, recent studies in Arabidopsis have revealed that lignin is formed, not at the RECs, but at the SECs, the AZ attached to the shedding organ  $[3^{\bullet\bullet}]$  suggesting a role of lignin in the process of abscission. Inhibition of lignification at SECs by drugs or genetic mutation disturbs the spatial arrangement of the cell wall enzymes and leads to their diffusion beyond AZ, which induces random segregation of SECs, delays abscission, and increases the vulnerability of AZ to the pathogen infection [3<sup>••</sup>]. These results suggest that the lignified cell wall provides spatial guidance to the cell-wall-hydrolyzing enzymes to restrict their reaction to a specific site, which is important for spatiotemporal regulation of abscission and subsequent surface integrity after abscission. Lignification in SECs was also observed in cauline leaves of Arabidopsis and Ginkgo biloba [3"] and in the fruit of Citrus [4] suggesting that the involvement of lignin in the process of abscission is conserved across various plants.

The spatial patterning of lignin is orchestrated by two antagonistic pathways, the pathway leading to and inhibiting lignin formation. Many efforts have been made to understand the mechanisms of localized lignin deposition [29]. However, our knowledge of transcription networks that regulate SEC-specific lignin formation is still obscure. One clue can be found in the study of the transcription factor BREVIPEDICELLUS (BP, also known as KNAT1), which negatively regulates the formation of lignin at the inflorescence stem [30]. BP/ KNAT1 has been shown to act downstream of the signaling pathway mediated by IDA and HAE/HSL2 independent of SEC-lignin formation [3°,31,32]. However, RECpreferential expression of *BP/KNAT1* leaves room for the possibility that BP/KNAT1 regulates abscission in part by modulating lignin metabolism [3°].

In tomato, AZ develops at the midpoint of the pedicel where the vasculature is heavily lignified (Figure 2). AZ development is directly linked to the suppression of lignification at the vascular tissue surrounding AZ, ensuring that AZ is a lignin-free area. Mutations in the MADSbox transcription factors, such as MACROCALYX, JOINTLESS, or MBP21, suppress the development of pedicel AZ, which in turn leads to continuously lignified vascular tissue and inhibits abscission [33,34]. Similarly, repression of lignin is observed in rice seed AZ (Figure 2). Seed shattering in rice is directly linked to grain yield, and the degree of grain shattering is greatly reduced during crop domestication. In the current rice-breeding programs, the seed-shattering habit is still a target, especially in *indica* cultivars that generally display a more easyshattering phenotype than *japonica* cultivars [35]. In rice, the AZ consists of a few layers of cells between the grain and the pedicel, where epidermal cells and the sclerenchyma of vascular tissues are heavily lignified [9,36]. One





Repression of lignin at the AZ in tomato and rice.

Illustrations display lignin distribution around the AZ of abscising alleles and non-abscising alleles in tomato and rice. Lignified cells are marked in red.

lignin-free layer is a predominant cellular feature of the pedicel AZ in a shattering-type *indica* cultivar, 'Kasalath', contrary to the continuously lignified sterile lemma and rudimentary glume, which connect at the pedicel AZ in the moderate-shattering 'Dongjin' and the non-shattering 'Ilpum' (japonica cultivars) [36]. The OSH15-SH5 complex regulates lignin biosynthesis in rice directly by repressing the expression of CAD2, encoding one of the lignin biosynthesis enzymes [5,36]. OSH15 is preferentially expressed at the AZ during spikelet development, while downregulation of OSH15 in cv. Kasalath fills the AZ with lignin and reduces the seed-shattering phenotype [5<sup>•</sup>]. These results suggest that securing a space devoid of lignin in the AZ is critical in species in which tissues are heavily lignified, and that a lignin-free layer is achieved by actively repressing the production of lignin. Specific functions of plant cells are often associated with local lignin formation [37-39], and understanding the regulatory mechanisms underlying the distribution of lignin around the AZ should provide additional insights into the roles of lignin in plants.

# Cell expansion and mechanical signaling during abscission

One of the notable features of RECs is longitudinal expansion, though the biological relevance of this phenomenon is not well understood. The longitudinal expansion of RECs is prominent during abscission, but is also noticeable before abscission [40]. Recent studies on lateral root development provide an evidence for the biological function of such volume changes [41<sup>••</sup>,42]. Initiation and growth of lateral roots are controlled by mechanical communication between pericycle and endodermal cells involving volume changes on both sides of cells and auxin signaling. Initial swelling of the lateral root founder cell acts as a mechanical stress for the overlying endodermal cells, which in turn induces controlled volume loss of endodermal cells providing room for emergence of lateral roots [41...]. These findings show the ability of plants to use turgor and/or volume change for cell-to-cell communications [38], which might be widespread in cellular responses including abscission. Interestingly, the IDA-HAE/HSL2 signaling module that activates floral organ abscission also mediates auxininduced cell wall remodeling of overlying cells during lateral root emergence [43<sup>•</sup>]. A deeper understanding on mechanical communication in abscission would provide more complete picture of the signaling networks of cell separation. Further investigation is needed to address the open questions, including whether swelling of AZ cells causes mechanical stress, if so, how the mechanical stress is perceived by neighboring cells, and how it acts as an upstream regulator of IDA.

In the 19th century, mechanical pressure derived by the expansion of AZ cells was regarded as a primary cause of cell separation [44,45]. This theory was forgotten once the

effects of cell wall hydrolases on abscission were demonstrated, and it is now widely accepted that cell wall hydrolysis is the cause of cell separation [19,20]; this has left the cell expansion feature an 'orphan'. Even after the middle lamella has dissociated, the leaves remain attached due to the vascular strands, which are believed to be easily broken due to wind or self-weight. Although widely believed, how easily lignified xylem can be broken due to external factors remains unclear: moreover, it is unlikely that the plant would rely exclusively on external factors for the final step of separation. Previous studies provided a different view on the same. Wiesner [46] showed that, when all the tissues except for the xylem of the petiole AZ were cut, the leaves did not fall off due to wind or weight. This implies that wind and weight cannot shed leaves without reducing the integrity of xylem. Sexton and Redshaw [47] revealed the stretched and ruptured spiral structure of xylem vessels on the fracture face of AZ in Impatiens sultani leaves and suggested the roles of cell expansion directed along the axis of the petiole during abscission in the rupture of the last remaining xylem vessels. Recently, Patharkar and Walker [48] provided evidence supporting this hypothesis. The authors demonstrated that water stress induced the abscission of Arabidopsis cauline leaves, an effect which occurred only after the plants were re-watered [48]. This suggested that water is an essential element in the abscission process. Although the authors did not provide a direct link between rehydration and cell expansion, it would be a reasonable assumption that rehydration leads to the expansion of AZ cells, which in turn promotes abscission. If so, SECs, which are bound together by lignin, would be the solid foundation against which the expanding RECs could press.

Recently, it has been shown that the explosive seed dispersal in Cardamine hirsuta relies on the hinged geometry of lignin in the endocarp b cell layer [37], showing elaborate utilization of lignin in cellular mechanics. Even in non-explosive fruits of Arabidopsis thaliana, precise patterning of fruit tissues is critical for seed dispersion, with the lignin arrangement at its core [49]. Differential mechanical properties of lignified and non-lignified tissues generate tension that triggers the opening of the fruit, and details of the molecular mechanism for this can be found in recent reviews [50,51]. Considering the genetic networks shared by seed abscission and fruit dehiscence, Balanza et al. suggested that fruit dehiscence may have evolved from the mechanisms controlling seed abscission [52]. Further understanding on similarity and difference between seed abscission and fruit dehiscence could bring deeper insights to the evolutionary variation to drive morphological and functional innovation.

### **Protective layer formation**

RECs form the outermost cell layers after abscission, suggesting their critical role in protecting the cell surface.

During abscission of woody plants, the protective layer and the periderm (associated with the periderm of stem) form underneath the separation layer [6,53]. These layers are suberized and provide a protective barrier, which is similar to the wound-induced periderm that is followed by suberization and lignification [54,55]. Intriguingly, the formation of a protective layer in floral organ AZ in Arabidopsis differs from these periderm-associated protective layers in that the remained AZ cells after abscission are converted directly into an epidermis-like protective layer [3<sup>••</sup>]. In most eudicots and gymnosperms, periderm arises during secondary growth and replaces the epidermis as the frontier tissue, a phenomenon which is also observed in Arabidopsis hypocotyls and roots [56<sup>••</sup>,57]. However, no periderm formation has been reported in the Arabidopsis stem, even in the stem of six-month-old plants of the soc1 full double mutant that have undergone extensive secondary growth [56<sup>••</sup>,58]. It is intriguing how protective layer formation would occur in tissues where the process of periderm formation is not inherent, such as in Arabidopsis stem. A recent study showing cuticle formation on the newly exposed cell surface following the abscission of floral organs in Arabidopsis suggests transdifferentiation of AZ cells into the epidermis as an alternative way to form protective layer without periderm-associated cell division [3<sup>••</sup>]. Further investigation of the molecular mechanisms of transdifferentiation in AZ cells and the comparative analysis of wound healing and programmed abscission would provide a broader insight into protection mechanisms in plants.

### Conclusions

Abscission is an important element in the strategy that enables a plant to adapt to the environment in a way that continuously creates new organs. Recent studies have shown that precise and complex signaling processes and remodeling of cellular activities and architectures are involved in this process, suggesting AZ to be an attractive model system to study cellular dynamics and cell wall remodeling. Abscission is directly linked with crop yield and has been an important trait in plant biotechnology in various crops including rice, tomato, legume, cassava, *Citrus*, and sugarcane [4,5°,59–63]. A multidisciplinary study using AZ as a model system would contribute to understanding the basic principles of plant cells, which can be applied to various fields of application.

### **Conflict of interest statement**

Nothing declared.

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