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RECEIVED 12 January 2024

ACCEPTED 08 February 2024

PUBLISHED 26 February 2024

## CITATION

Baba AI and Verger S (2024) Cell  
adhesion maintenance and  
controlled separation in plants.  
*Front. Plant Physiol.* 2:1369575.  
doi: 10.3389/fpphy.2024.1369575

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# Cell adhesion maintenance and controlled separation in plants

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Cell-cell adhesion is a fundamental aspect of maintaining multicellular integrity while ensuring controlled cell and organ shedding, intercellular space formation and intrusive growth. Understanding of the precise mechanisms governing regulated cell separation, such as abscission, considerably progressed in recent decades. However, our comprehension of how plants maintain adhesion within tissues in which it is essential remains limited. Here we review some of the well-established knowledge along with latest discoveries that lead us to rethink the way developmentally controlled cell separation and adhesion maintenance may work. We also specifically explore the relationship between growth and adhesion, highlighting their similarities and coupling, and propose a plausible framework in which growth and adhesion are tightly co-regulated.

## KEYWORDS

adhesion, cell wall, abscission, separation, growth

## Introduction

Plants are multicellular organisms that exhibit clonal multicellularity and develop from a single cell through the process of cell division. Contrary to animal, plant cells are surrounded by a cell wall which mediates their adhesion (Atakhani et al., 2022). Adhesion between cells is established during cell division when a new shared wall is formed by the cell plate (Jarvis et al., 2003). Throughout normal growth and development, cell differentiation gives rise to a complex tissue organization roughly made up of the epidermis, ground tissues, vasculature, and meristems. Interestingly, different tissues appear to develop differential adhesion. While the epidermis keeps a strong adhesion to form a barrier to the environment (Galleggi et al., 2016), stomata formed within it through guard cells separation allow a controlled gas exchange between the inside and outside of the leaf (Lin et al., 2022). Below the epidermis, the mesophyll and cortex parenchyma (types of ground tissue) tend to develop large intercellular spaces forming largely by cell separation at the tricellular junctions (Whitewoods, 2021). This creates a large network of air spaces in the tissues that is important for gas exchange and photosynthesis (Figure 1F). Further within the tissues, the vasculature tends to develop rigid and thickened cell walls with tight adhesion to ensure the proper transport of water and nutrients (Kuriyama and Fukuda, 2007; Lucas et al., 2013). Later on, a number of cells and organs can shed through cell separation. For instance, leaves as well as floral organs such as sepal, petal, stamen and carpels

undergo abscission after pollination and seed maturation (Figure 1A; Leslie et al., 2007). The seeds can shed, and the pollen grains separate to be disseminated individually (Figure 1D; Wen et al., 2007). In the root system, root cap sloughing and border cells separation from the root tip help to protect the root and promote soil penetration (Figure 1C; Driouich et al., 2007; Wen et al., 2007). In parallel, lateral roots emerge through the cortex and epidermis thanks to controlled cell separation (Figure 1B; Banda et al., 2019). Some specific cell types such as the pollen tube and fiber cells can grow intrusively by their tip, leading to cell-cell contact rearrangement (Figure 1E; Mollet et al., 2007; Marsollier and Ingram, 2018). Finally, cells can re-adhere through grafting or post embryonic tissue fusion (Melnyk, 2017). This brief overview of cell adhesion and separation dynamics in plants highlights how important the regulation of cell adhesion is for plant growth and development (Figure 1).

## Cell adhesion is mediated by the cell wall

The attachment of neighboring cells in plants is mediated through the formation of the cell wall. Approximately 90% of the

total components in the cell wall are made up of polysaccharides, namely cellulose, hemicellulose, and pectin, along with structural proteins and cell wall remodeling enzymes making up the remaining 10% (Anderson and Kieber, 2020). In young expanding tissues the cell wall between two adjacent cells generally displays a layered structure: at the center the middle lamella is enriched in pectins, and on each side sit the primary cell walls of each adjacent cells. This structure is believed to be established during and following cell division (Jarvis et al., 2003). First, when the formation of the cell plate establishes the precursor of the middle lamella, and after the completion of the new cell wall when each daughter cells initiate the synthesis of their primary cell wall (Zamil and Geitmann, 2017). These newly formed walls thus sandwich the pre-existing pectin-enriched matrix derived from the cell plate that forms the middle lamella. Note that the exact genesis/origin, structure and composition of the middle lamella remains poorly understood (Zamil and Geitmann, 2017; Malek and Mouille, 2023). Yet, overall, it is generally recognized that pectins and the middle lamella play a central role as components of the cell wall for mediating cell adhesion (for extensive reviews on the topic see Knox, 1992; Jarvis

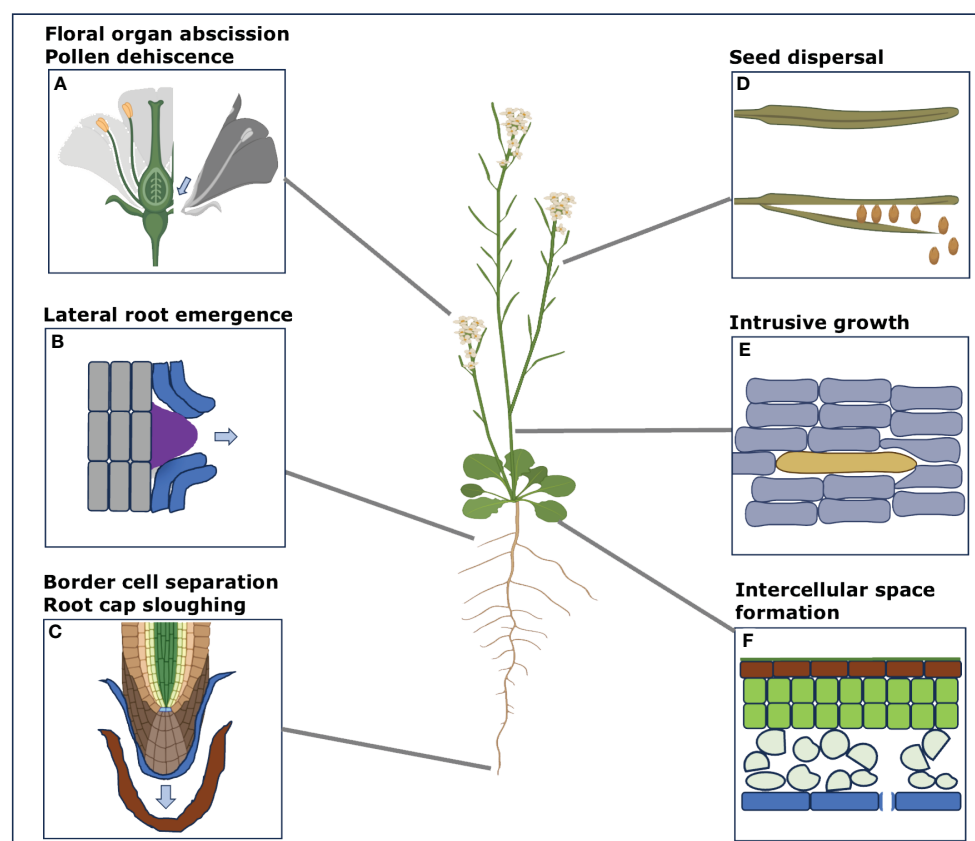


FIGURE 1

Different examples of the processes involving cell separation in the model plant *Arabidopsis*. Here, we display some of the main processes that involve cell separation during various developmental stages and during specific periodic changes in *Arabidopsis*, used as an example here. These processes are not just limited to this model species only but can be involved in other plant species too. These different instances of cell separation processes include (A) Floral organ abscission of sepals, petals, stamens, carpels including pollen separation (B) Lateral root emergence through the cell layers of cortex and epidermis (C) Root cap sloughing and border cell separation from the root tip (D) Seed dispersal after the maturation from the siliques (E) Intrusive growth of cambial cells in inflorescence stems (F) Intercellular space formation in the mesophyll and cortex parenchyma. (Some segments from this figure were generated with the help of Biorender ([www.biorender.com](http://www.biorender.com)) accessed on 14 December 2023).

et al., 2003; Daher and Braybrook, 2015; Atakhani et al., 2022). The middle lamella can then be specifically degraded through the action of pectin remodeling and degrading enzymes (e.g. Pectin Methyl Esterases (PMEs), PolyGalacturonases (PGs) and Pectate Lyases (PLs)) for cell separation (Daher and Braybrook, 2015). Interestingly, the pectin in the middle lamella is often depicted as the glue that makes the cells stick together (Zamil and Geitmann, 2017). However, except in specific cases (e.g. grafting) plant cells are not adhering to each other by being put in contact to stick but rather remain attached after cell division. In turn, it could be argued that instead of being a “gluing layer”, the middle lamella may primarily serve as a “degradable” layer for cell separation, that can specifically be degraded by a subset of enzymes (pectin degrading), without degrading the whole cell wall which would otherwise threaten cell integrity.

The primary cell wall also serves a central role in cell and tissue growth. It is a dynamic structure that is constantly remodeled during the processes of growth and development (Anderson and Kieber, 2020; Cosgrove, 2023). This is mediated by the constant synthesis and secretion of cell wall polysaccharides and proteins. This contributes to adding material to the wall while it is being expanded and to remodel it to allow changes of extensibility (Anderson and Kieber, 2020). Along with turgor pressure, the action of cell wall remodeling enzymes has been shown to be the key downstream mediator of cell expansion, overall controlling tissue growth and morphogenesis (Cosgrove, 2022; Coen and Cosgrove, 2023). Those enzymes typically include members from the XYLOGLUCAN ENDOTRANSGLUCOSYLASE/HYDROLASE (XTH), EXPANSIN (EXP), CELLULASE, PECTIN METHYLESTERASE (PME) and POLYGALATURONASE (PG) families (For a comprehensive review on the subject see Cosgrove, 2016). For growth to be properly regulated, the action of these enzymes should not lead to the overall degradation and excessive weakening of the cell wall, which could lead to cell bursting due to turgor pressure (Feng et al., 2018; Sapala et al., 2018; Malivert et al., 2021). Instead, the activity of these enzymes and overall cell wall remodeling needs to be tightly regulated by cell wall integrity signaling feedback mechanisms (Bacete and Hamann, 2020). Interestingly there are striking similarities in the set of cell wall remodeling enzymes that are involved in growth and cell separation (See sections below). This could imply that similar cell wall integrity mechanisms could be in place not only for keeping cellular integrity (preventing cell bursting) but also keeping supracellular integrity (cell adhesion) (Verger et al., 2018) during extensive growth.

## Developmentally controlled cell separation in plants

As described in the introductory section, there are several events throughout plant life during which cell separation is specifically triggered (Figure 1). The process of abscission has been particularly studied for its agricultural implications. Here we provide a broad description and the common mechanisms regulating these types of developmentally regulated cell separation, but for more detailed review see (Ballester and Ferrándiz, 2017; Patharkar and Walker,

2018). Broadly, abscission processes can be categorized into four stages: 1) Initially, abscission in plants involves the formation of a defined Abscission Zone (AZ) with the specification of specialized cell layers mediated by developmental patterning transcription factors (Mao et al., 2000; Cho et al., 2008; Gubert et al., 2014). 2) The second step consists in triggering the signaling cascade that will lead to cell separation in the abscission zone. A precise balance between ethylene and auxin has been shown to be key in triggering abscission and may serve to integrate environmental stimuli to regulate the timing of abscission (Taylor and Whitelaw, 2001; Butenko et al., 2006; Meir et al., 2010). Moreover, the non-hormonal control of abscission in plants involves the short secretory peptide known as INFLORESCENCE DEFICIENT IN ABCISSION (IDA) (Butenko et al., 2003) and its downstream receptor-like kinases (RLKs), HAESA (HAE) and HAESA-LIKE 2 (HSL2) (Cho et al., 2008; Estornell et al., 2015). Downstream, this peptide-receptor complex activates a mitogen-activated protein kinase (MAPK) cascade, which primarily consists of MAPK kinase 4 (MKK4)/MKK5 and MAPK 3 (MPK3)/MPK6 (Cho et al., 2008), and may ultimately de-repress the transcription factors KNOTTED-LIKE FROM ARABIDOPSIS THALIANA2 (KNAT2) and KNAT6 (Shi et al., 2011). 3) This signaling cascade then leads to the massive expression of cell wall remodeling enzymes. While the pectin remodeling enzyme of the PME and PG families have been shown to be central players for cell separation, it was also shown that a wider set of CWR enzyme is expressed during abscission. Those enzymes typically include members from the XTH, EXPANSIN, CELLULASE, PME and PG families (Cho and Cosgrove, 2000; Rhee et al., 2003; Francis et al., 2006; Cai and Lashbrook, 2008; Ogawa et al., 2009). Interestingly, the combined action of these enzymes, along with the presence of turgor pressure in the cells also lead to local cell expansion (Cai and Lashbrook, 2008) and overall generate forces that physically help pull cells apart to achieve abscission (Reiche, 1885; Taesakul et al., 2015). Finally, 4) after the abscission of the organ, a protective epidermal layer is formed at the abscised region in the plant (Shi et al., 2019).

Interestingly, some of the cell separation processes taking place in the root, namely lateral root emergence and root cap sloughing have also been shown to involve part of the IDA signaling cascade without apparent abscission zone specification. For lateral root emergence, auxin signaling was shown to induce the expression of the IDA peptide around the lateral root emergence site, which along with the HEA and HSL2 receptors, help the lateral root primordia to emerge from different cell layers (Kumpf et al., 2013). The IDL1 (IDA LIKE1) homologs of IDA and its receptor HSL2 have been shown to regulate root cap sloughing by controlling the frequency of sloughing events (Shi et al., 2018). Interestingly however, the progressive detachment of the border-like cells along the elongating root tip seems to happen independently from the sloughing events. Overall, this suggests that the IDA/HEA signaling module may be widely employed to specifically trigger cell separation events in plants. Note however, that there are significant differences in the way in which root cap cells detach between different species. Arabidopsis and more generally Brassicaceae represent a specific case for which border cells do

not fully detach (Border-like cells; (Driouich et al., 2007; Mravec et al., 2014)) while in other species, true border cells are continuously released as individual cells (Mravec, 2017; Mravec et al., 2017) and thus may not require active root cap sloughing-off events.

## Active rearrangement of cell adhesion by intrusive growth

By far most cells in plant tissues establish adhesion during cell division and grow in a diffuse symplastic manner, keeping the same neighbors throughout their life span. However, some specific cell types harbor an intrusive tip growth behavior leading to the rearrangement of cell-cell contacts. The two most studied examples of intrusive tip growth in plants are the pollen tubes (Kamel and Geitmann, 2023) and the fiber cells (Lev-Yadun, 2001; Gorshkova et al., 2012). During intrusive tip growth, cells generally elongate specifically at their tip by a combination of the addition of cell wall material localized at the tip and internal hydrostatic (turgor) pressure (Sanati Nezhad and Geitmann, 2013). Different pectin modifying enzymes are believed to be implicated in the modification of the cell wall during pollen tube growth (Bosch and Hepler, 2005; Kamel and Geitmann, 2023). Recently it was shown that pectate lyase-like (PLL) may contribute to the lubrication and loosening of the middle lamella in the intruded tissues (Chebli and Geitmann, 2023). In wood fiber cells, several studies have revealed the contribution of cell wall remodeling enzymes. Those include the XTH, EXPANSIN, PME and PL families (Im et al., 2000; Israelsson et al., 2003; Gray-Mitsumune et al., 2004; Gray-Mitsumune et al., 2008; Siedlecka et al., 2008; Kushwah et al., 2020). It is generally unclear if those enzymes primarily play a role in the cell wall remodeling at the tip for tip growth or specifically contribute to loosening the middle lamella of the intruded tissues, but it is worth considering that some of these enzymes may serve both purposes at the same time. In addition to cell wall remodeling, physical factors also play a major role. It has been shown that the turgor pressure in the growing tip of pollen tubes applies considerable forces that help penetrating between the cells (Sanati Nezhad et al., 2013). It was also proposed that high turgor pressure and radial expansion of the cells making up the tissues in which cells intrude may contribute to promote intercellular spaces formation. The intruding tips could then grow more easily within such intercellular spaces (Yanagisawa et al., 2017; Majda et al., 2021).

## Intercellular spaces formation

Plant internal tissues can develop air spaces which are notably important for gas exchange and photosynthesis (Earles et al., 2018; Whitewoods, 2021). In most cases they initially form by cell separation at the tricellular junctions. Air spaces can further expand by continued cell separation (schizogeny), through the expansion of the already separated wall regions (expansigeny) or a combination of both (Zhang et al., 2021), which leads to an

increase in airspace size (Whitewoods, 2021). Interestingly this process is tightly associated with the intense expansion of the tissues in which it takes place such as during leaf and stem expansion. In this case it is still unknown which cell wall remodeling enzymes are involved in the initial cell separation process. However, the high turgor pressure in those ground tissues that is required to drive tissue growth (Kutschera and Niklas, 2007) should play a key role. At tricellular junction, cell edges often display sharp angles. Because the cortical (cell wall) tension derived from turgor pressure would tend to round up those edges, in fully adhering cells, those tricellular junction are mechanical stress hotspots that contribute to separate the cells if adhesion is weakened (Jarvis, 1998; Treado et al., 2022). In turn, it is possible that growth-promoting cell wall remodeling enzymes activity in combination with high separation forces at those mechanical hotspots would be sufficient to weaken the middle lamella to a point that would allow cell separation at tricellular junctions. Interestingly, in this case cell separation would be a passive process, collateral to the process of growth.

## Cell adhesion maintenance: the case of cell adhesion defective mutants

As described above, while many cells in ground tissues develop intercellular spaces through partial cell separation, other surrounding tissues like the epidermis and vasculature need to maintain tight adhesion. However, the mechanisms regulating these processes are still very unclear. Within the last three decades, genetic screens have led to the isolation of cell adhesion defective mutants which are thus unable to properly maintain adhesion and offer some clues to start investigating this process. Such mutants could either be unable to produce the cell wall polysaccharides that keep cells attached to each other or be involved in sensing and feedback mechanisms ensuring the maintenance of adhesion. One of the most characteristic examples are the *quasimodo1* (*qua1*) and *qua2* mutants (Bouton et al., 2002; Krupková et al., 2007; Mouille et al., 2007), for which the disrupted loci encode a putative galacturonosyltransferase and a pectin methyltransferase (Du et al., 2020), respectively. These mutants are deficient in HomoGalacturonans synthesis (HG), the main form of pectin in the cell wall and middle lamella. This led to the conclusion that the adhesion phenotype of these mutants was a direct consequence of decreased pectin content in the cell wall, likely disrupting the middle lamella. However, a genetic suppressor screen carried out on both *qua1* and *qua2* mutants identified alleles of *ESMERALDA1* (*ESMD1*), a putative o-fucosyltransferase (Verger et al., 2016). The suppressor lines display a rescued adhesion phenotype without restoring the HG fraction that is deficient in the *quasimodo* mutants. *ESMD1* was hypothesized to play a role in cell wall integrity sensing, via the pectin-binding receptor WALL-ASSOCIATED KINASES (WAKs) by potentially mediating the o-fucosylation of the epidermal growth factor (EGF) domains of the WAKs (Verger et al., 2016). Another putative o-fucosyltransferase mutant, *friable1* (*frb1*) was shown to have cell adhesion defects

without significant pectin levels deficiency except for a perturbed HG methylesterification level (Neumetzler et al., 2012). Altogether this suggests that bulk pectin content in the cell wall may not be the primary determinant of cell adhesion maintenance, but that more complex regulations of the pectin and overall cell wall structure are at play. However, it was later shown that enzymes of the putative o-fucosyltransferase family, including FRB1 are instead acting as Rhamnose RamnosylTransferases (Takenaka et al., 2018; Wachananawat et al., 2020) and thus involved in the synthesis of RGI pectins rather than signaling. It was also shown that WAKs are likely not o-fucosylated on their EGF domains, that *esmd1* does not seem to impact the function of the WAKs, and that knocking out WAKs did not rescue adhesion defects in the *qua2* mutant (Kohorn et al., 2021). Nevertheless, further work confirmed that the *QUA2* knockout does lead to massive secondary responses which can largely account for its phenotypes and that most are absent in the *qua2 esmd1* suppressor line. These includes over expression of PGs, miss regulation of PME as well as deficiency in cellulose synthesis and a disrupted cuticle (Du et al., 2020; Lorrai et al., 2021; Barnes et al., 2022; Grandjean et al., 2023). It was also recently suggested that endogenous oligogalacturonides (small pectin fragments derived from the degradation of HG) may play a signaling role in this context (Grandjean et al., 2023). Furthermore, an *esmd1* mutant allele was also recently isolated as a suppressor of the cellulose deficient mutant *korrikan1* (*kor1*). In this case it appears to act by suppressing elevated jasmonate levels in the *kor1* mutant (Mielke et al., 2021). While it is still unclear what the function of ESMD1 is, these observations suggest that ESMD1 may still play a role directly or indirectly in cell wall integrity signaling which ultimately influences cell adhesion maintenance.

It is also interesting to note that the *quasimodo* adhesion phenotype can be partially rescued by decreasing the overall growth or the tissue tensions derived from differential growth between the inner tissues and the epidermis (Verger et al., 2018) and that it can be enhanced by increasing the growth differential between the inner tissues and epidermis (Kelly-Bellow et al., 2023). This shows that in *quasimodo*, in addition to a reduced adhesion mediated by extensive cell wall remodeling, the adhesion phenotype depends on the overall extent of growth and tension pulling cells apart in the epidermis.

In addition to *QUA1*, *QUA2*, *ESMD1*, and *FRB1*, two new gene families have recently been identified to act in the same pathway. Mutation in the genes coding for Golgi membrane localized protein ELMO1, ELMO2 and ELMO4/NKS1 (Kohorn et al., 2021; Lathe et al., 2021) as well as Golgi-localized putative S-adenosyl methionine transporters (GoSAMT1 and GoSAMT2) (Temple et al., 2022) also lead to a strong defect in cell-cell adhesion which can be rescued by *esmd1*. ELMO family proteins are suspected to act as scaffold for *QUA1* and *QUA2* in the Golgi (Lathe et al., 2021; Kohorn et al., 2023) and GoSAMT transporter should be necessary to provide the S-adenosyl methionine for HG methyl esterification by *QUA2* in the Golgi.

Beyond direct cell wall regulators, other mutants with clear cell adhesion defects include mutants defective in actin filament

nucleators from the ACTIN-RELATED PROTEINS 2 and 3 (ARP2/3) complex (Le et al., 2003; Mathur et al., 2003) as well as upstream regulators SCAR/WAVE (WASP family Verprolin homolog — also known as SCAR for suppressor of cAMP receptor) complex (Basu et al., 2004; El-Assal et al., 2004) and SPIKE1 (Qiu et al., 2002). While these mutants do not appear to have clear cell wall defects in growing tissues (Dyachok et al., 2008; Pratap Sahi et al., 2017), they suggest a more localized role of actin-mediated cell wall polysaccharides secretion at the subcellular level for the proper maintenance of cell adhesion. Furthermore, the putative mechanosensitive calcium channel DEFECTIVE KERNEL1 (DEK1; Galletti et al., 2015; Amanda et al., 2016) and epidermal identity transcription factors MERISTEM LAYER1 (ATML1) and PROTODERMAL FACTOR2 (PDF2) mutants (Abe et al., 2003) show epidermis specific adhesion defects. While DEK1 phenotype suggests a role for mechanical signals feedback in regulating cell adhesion maintenance, it was also shown to contribute to epidermal cell identity (Johnson et al., 2005) and epidermal identity was shown to be regulated by mechanical signals (Iida et al., 2023). In *dek1* and *pdf2 atml1* mutants, cells that should belong to the epidermal cell layer, instead resemble mesophyll cell. This suggests that in these mutants the outer layer of cell has either lost the capacity to specifically maintain cell adhesion as the epidermis normally does, or that it activates a putative signaling pathway leading to intercellular space formation. Overall, while they remain to be better characterized for their cell adhesion phenotype, these mutants further hint at a complex regulation of cell adhesion maintenance in plants through cytoskeleton dynamics, cell wall integrity, mechanosensing and cell identity specification.

## Growth and adhesion

Based on the above review of the field it appears that there are likely at least two separate mechanisms regulating cell adhesion in plants. One specifically to promote cell separation and one specifically to maintain cell adhesion. It is well established that for active cell separation events such as in the case of abscission, upstream control by hormones and peptides lead to the specific and active digestion of the cell wall (see section *Developmentally controlled cell separation in plants*). One could argue that in this context the extensive cell wall remodeling that is taking place is aimed at cell separation but with the collateral action of promoting local expansion that in turn helps to pull cells apart. This tends to support the idea that adhesion between cells is a passive default state initially established during cell division, and that an active mechanism needs to be triggered to induce separation. However, it is important to note that these events take place in tissues which are not actively growing anymore. It is thus necessary for the plant to specifically re-activate cell wall remodeling that can lead to the digestion of the middle lamella, but also differential growth between different parts of the abscission zone to help physically pull the cells apart. In other words, cell separation needs a combination of cell

wall remodeling, growth, and tensions to take place. On the other hand, similar conditions are already present by default in actively growing tissues. The process of growth is driven by turgor pressure which, along with cell wall remodeling, generates cell expansion (Cosgrove, 2016). It is also well established that the layered tissue organization leads to tissue tensions: high tension in the growth restricting epidermis, and relative compression in the inner tissues (Kutschera and Niklas, 2007). Work on cell adhesion defective mutants has further revealed that cell separation in those mutants is largely correlated with the extent of growth-derived tissue stresses (Verger et al., 2018; Kelly-Bellow et al., 2023). In turn, this supports the idea that in growing tissues, adhesion is not a default state. Growth associated mechanisms actively remodel the cell wall and tend to pull epidermal cells apart. Thus, plants may need to put specific mechanisms in place to prevent cell separation in cell types where adhesion is threatened and needs to be maintained. In this framework, plants would need a cell separation pathway in non-growing tissues (e.g. abscission) and a cell type specific adhesion maintenance pathway in growing tissues (Figure 2).

## Revisiting the relationship between adhesion and separation in the context of growth

With this in mind we can revisit some of the cases mentioned in the sections above where adhesion is dynamically regulated including those for which we still know very little regarding their regulation mechanisms. Classical abscission and dehiscence events (leaves, floral organs, seed shedding, etc.) are already well described and take place in non-growing tissues, thus are less ambiguous in this regard. On the other hand, the case of intercellular space formation takes place in actively growing tissues and the mechanisms regulating it are still unknown. To our knowledge, none of the abscission deficient mutants are affected in intercellular space formation suggesting that it may not require such pathway. The initiation of intercellular spaces may instead be largely collateral to growth-associated cell wall remodeling and tensions at the tricellular junctions. Because adhesion remains tight in the

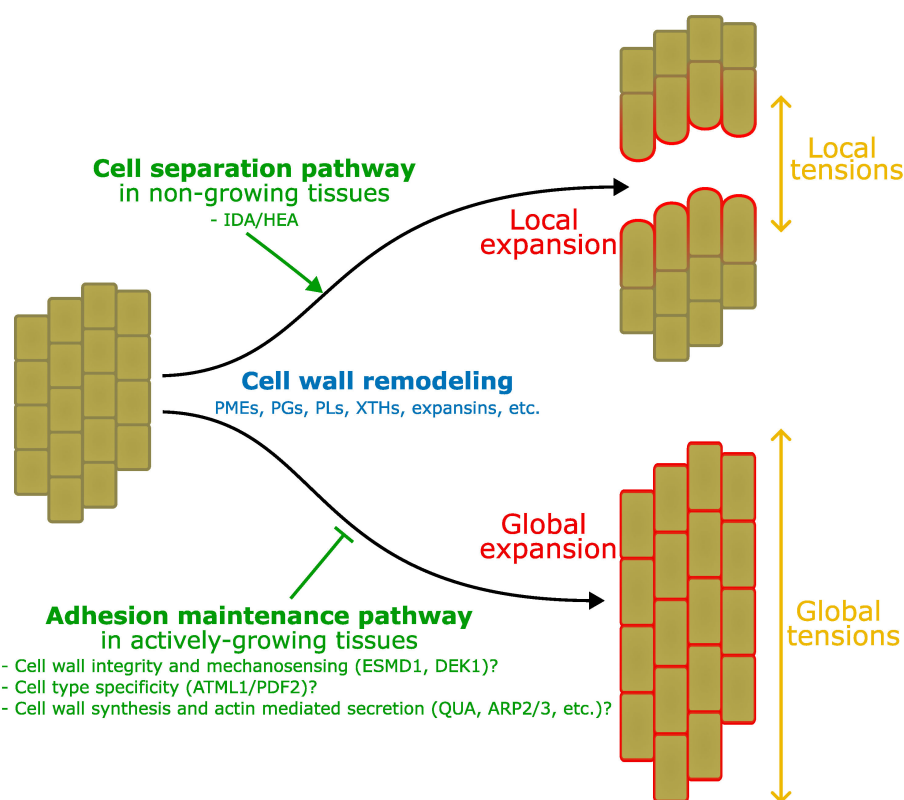


FIGURE 2

Interplay between adhesion, growth and tension. Here we take as an example the comparison between the process of abscission and growth in elongating tissues. In this schematic representation, both start from a group of fully adhering short cells (left). On top, IDA/HEA mediated abscission mechanisms induce local cell wall remodeling in the abscission zone (not represented), expansion and tensions, that lead to local cell separation. Below, growth induction also involves global cell wall remodeling, expansion, and tissue tensions, however, adhesion maintenance mechanisms may prevent cell separation that would otherwise takes place as suggested by mutants' studies. Those mechanisms may involve a combination of molecular players and processes: ESMD1 and DEK1 may be involved in cell wall integrity and mechanosensing to monitor the state of the cell wall in relation to adhesion during growth. ATML1 and PDF2 epidermal identity specification may limit the activity of the adhesion maintenance pathway to the epidermis only. Wall integrity, mechanosensing and cell identity may contribute to regulate cell wall synthesis (QUA, FRB, GoSAMT, ELMO), and actin mediated secretion (ARP2/3, SCAR/WAVE, SPIKE), to ensure cell adhesion in the epidermis during growth. Similar mechanisms may for instance be at play in the vasculature, while ground tissues can develop intercellular spaces.

epidermis, keeping all inner tissues cells within a sort of epidermal envelop, partially loosing adhesion between ground tissue cells doesn't threaten the supracellular integrity of the organism. Then, the only control of cell adhesion needed would be for the maintenance in the epidermis and vasculature. While the molecular bases of such an adhesion maintenance pathway are still unclear, it could rely on cell wall integrity, mechanosensing mechanisms and be influenced by cell identity as suggested by the study of cell adhesion defective mutants (see section *Cell adhesion maintenance: The case of cell adhesion defective mutants*). The case of intrusive tip growth is quite interesting since it is by itself directly coupled with growth. It also takes place in tissues which are still growing and that develop intercellular spaces for the intrusive tip to grow in between (Majda et al., 2021). It is thus possible that the simple process of tip growth and associated cell wall remodeling enzyme secretion (Chebli and Geitmann, 2023) along with formation of growth associated intercellular spaces (Majda et al., 2021), is enough to explain the phenomenon of intrusive tip growth without the need for specific cell adhesion regulation mechanism. On the other hand, lateral root emergence can sometimes be considered as a case of multicellular intrusive growth. However, while the lateral root tip does grow, the emergence has to take place through the mature root cortex and epidermis which are not growing anymore. The tip of the lateral root has also been shown to be covered with a thin cuticle layer (Berhin et al., 2019). While it appears to help lubricating the tip for the root emergence, it would also prevent the secretion of cell wall remodeling enzymes by the growing root tip contrary to what has been shown for the pollen tube intrusive growth. In turn, cells of the cortex and epidermis within which the root will emerge, have to activate an abscission-like pathway that specifically triggers their separations. Finally, the case of the root cap cells is also particularly interesting. In the Arabidopsis growing root tip, the continuous detachment of the so-called border-like cells and the sloughing off of the root cap involves the separation of cells, but these appear to be two separate mechanisms at play. The border-like cells along the growing root tip appear to progressively detach as the root grows, and in parallel there is a periodic sloughing off of entire cell layers. While it has been shown that the periodic sloughing off events are regulated by a specific abscission pathway, it is likely that the progressive border-like cell detachment is a collateral effect of the root tip growth associated with the fact these cells enter a programmed cell death (Feng et al., 2018) and may not be able to actively maintain their adhesion anymore. However, as mentioned previously, border-like cells represent a particular case that appears to be specific to Brassicaceae (Driouich et al., 2007). In other species, the border cells continuously detach as individual cells, remain alive and play a key role in the root-soil interaction (Hawes et al., 2000). Border cell detachment was shown to involve extensive cell wall remodeling notably by PME's but without noticeable pectin degradation by PGs or PLs (Mravec, 2017; Mravec et al., 2017). It was proposed that this remodeling would still contribute to loosen the middle lamella as well as drive differential growth, along with the asymmetric distribution of xyloglucans and extensins, between the inner and outer faces of border cells (relative to the root surface). This differential growth leads to the bending of individual cells which

physically promotes their detachment from the root surface (Mravec, 2017; Mravec et al., 2017). Interestingly this supports the idea that growth associated cell wall remodeling and tensions can be sufficient to alter cell adhesion even in the absence of extensive pectin degradation. This also suggest that contrary to border-like cells, border cell detachment does not require active abscission-like cell separation. In turn, simply lacking a specific adhesion maintenance mechanism for the root cap cells, in the context of root tip growth, could largely explain their detachment dynamics. It was also shown that inhibiting PME activity during border cell release led to an incomplete detachment of the cells similar to what is observed with border-like cells (Mravec et al., 2017). Brassicaceae may have lost the ability to fully detach border cells and instead co-opted abscission and programmed cell death pathways to balance their root cap proliferation.

## Are growth and cell separation mechanisms really similar?

Overall, here we highlight that the mechanisms of growth and cell separation appear to be highly similar in terms of cell wall remodeling and mechanics. Pushing this logic further, one could propose that abscission is only a precise targeted growth event in which adhesion maintenance feedback mechanisms are not active. There is, however, no clear evidence for that yet. Adhesion defective mutants appear to be a promising tool to study what could be the cell adhesion maintenance mechanisms. However, while here they are somehow depicted as potentially passively unable to maintain adhesion, the pectin deficient *quasimodo* mutant were for instance shown to not only have less pectin, but also an increase of pectin degradation by PME's and PG and other cell wall and cuticle defects (Du et al., 2020; Lorrai et al., 2021; Barnes et al., 2022; Grandjean et al., 2023) reminiscent to what takes place during abscission event. It is thus difficult to know if this relative increase in cell wall remodeling is in fact a sign of abscission-like event triggered throughout the plant in this mutant background or only a sign that such cell wall remodeling is normally down regulated by a functioning adhesion maintenance feedback mechanism. We also pointed out several times the similarities in terms of enzymes involved in growth and cell separation associated cell wall remodeling, but it is important to note that these enzymes are part of large families and that their activities can vary and lead to radically different effects. It is for instance proposed that some endogenous PGs have an effect specifically for expansion and other more specifically for cell separation (Ogawa et al., 2009; Xiao et al., 2017; Safran et al., 2023). Furthermore, in the long term, sustained growth also involves additional cell wall synthesis and secretion, that would compensate for some of the cell wall loosening and adhesion weakening effect of cell wall remodeling enzymes. Overall, such a difference in activities within enzyme families and presence or absence of cell wall synthesis could indicate that, although they appear similar, growth and cell separation mechanisms are really distinct processes. Nevertheless, these processes remain tightly linked, at least in terms of mechanics.

## Conclusion

While much progress has been achieved in the past to characterize the processes of abscission, recent work opened the door to study how adhesion maintenance may work. However, much remains to be done to better characterize what really is adhesion and adhesion maintenance in the case of plants. What sets apart adhesion deficiency from abscission? What is the contribution of the cell wall in the interplay between adhesion, growth, and development? Future work will need to integrate not only the molecular and chemical aspects of adhesion regulation but also the mechanics and in particular the coupling with growth.

## Author contributions

AB: Visualization, Writing – original draft, Writing – review & editing. SV: Conceptualization, Funding acquisition, Visualization, Writing – original draft, Writing – review & editing.

## Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. The author (s) would like to acknowledge the financial support from the Knut and Alice Wallenberg Foundation (KAW 2016.0341 and KAW 2016.0352), the Swedish Governmental Agency for Innovation Systems (VINNOVA 2016-00504) as well as a grant from the Novo Nordisk Foundation (NNF21OC0067282) to SV. We also

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thank Bio4Energy, a Strategic Research Environment supported through the Swedish Government's Strategic Research Area initiative, for supporting this work.

## Acknowledgments

We are grateful to Adrien Heyman, Asal Atakhani and Ioannis Theodorou for their helpful comments on the manuscript.

## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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