



REVIEW

Organ Abscission in Plants: With Special Emphasis on Bell Pepper

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ABSTRACT

Bell pepper (*Capsicum annuum* L.), along with potato and tomato, is one of the three most cultivated vegetables in the world. Bell pepper is worldwide accepted due to its characteristics of color, smell, flavor, and texture. Bell pepper is also considered a nutritious food due to its vitamin and antioxidant contents. In Mexico, bell pepper production has a high value because it is grown for the international markets, particularly the United States of America. Nevertheless, the abscission of flowers and fruits is a factor that limits the yield, hinders the planning of activities, and causes a variation in the prices of peppers. Due to the importance of this process, in this work we did a bibliometric analysis and literature review of scientific advances for the understanding of the abscission process in plants, and in particular for the bell pepper. Finally, we introduce new perspectives that would help direct future research about organ abscission in plants. Likewise, the lack of research that would further clarify abscission process in the bell pepper plant is discussed.

KEYWORDS

Capsicum annuum; abscission zone; plant growth regulators; environmental factors

1 Introduction

Plant reproductive organ abscission is an essential biological process and is an evolutionary mechanism generated in response to stress or environmental changes, because of external and internal signal induction or growth stages [1]. Horticulture can benefit from both enhancing or blocking abscission depending on the grower's needs [2].

Premature abscission (separation of plant organs) of flowers and fruits is a factor that limits the yield in horticultural crops [3]. Bell pepper crops, like other indeterminate greenhouse vegetable crops, present strong fluctuations in fruit harvesting patterns, in which periods of high yield alternate with periods of low yield [4,5]. The variability in the production and yield of bell peppers poses a challenge for the grower to plan activities throughout the production cycle. These yield fluctuations can also affect the price of bell peppers during the growing season [6].

Abscission in vegetable crops is related to factors including temperature, drought stress [7,8], reduced light conditions [9,10], and limited pollination [11]. However, bell pepper plants may also present abortion of



flowers and young fruits in non-limiting conditions, probably due to internal competition for nutrients (macro and micronutrients) [5].

A precise search into the studies focused on plant organ abscission will allow us to examine the evolution and attention given to the subject over the years. Accordingly, we carried out a simple research to quantify published scientific articles in the Scopus[®] scientific platform using the keywords: *organ abscission/plants* (Fig. 1) and were able to determine that the publications on this issue increased considerably from 2005 to 2023.

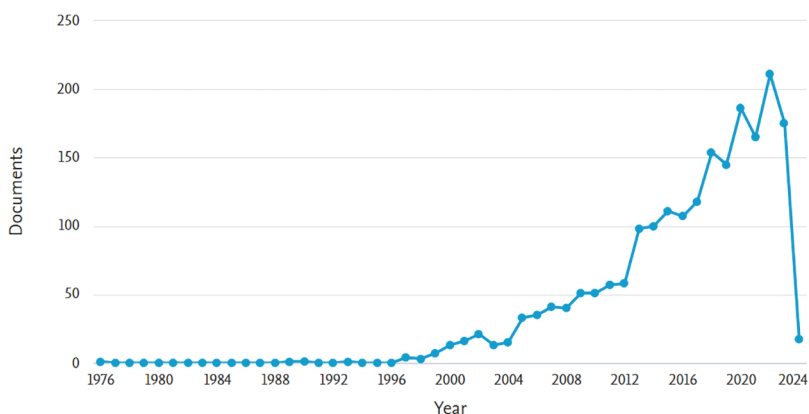


Figure 1: Scientific publications on plant organ abscission by year, from 1972 to 2024 based on the Scopus[®] scientific platform according to the following keywords: *organ abscission/plants*

The parametrization was done of scientific studies related to abscission in plants, the network visualized can be attributed to the keywords that appear most frequently in each published article (Fig. 2). These keywords served to identify the focus of the bibliographic study, which helps in providing answers and solutions to research problems [12]. The characterization of global network mapping was established and depicted the bibliographic map of keyword concurrence frequency using the scientific platform Scopus[®].

An image for the keyword's *organ abscission/plants* (Fig. 2) and another one for *Abscission/Capsicum* (Fig. 3) are portrayed.

The main keywords associated with the abscission process were “*Arabidopsis*,” “abscission,” “flowers,” “metabolism,” and “gene expression regulation.” The findings from this search suggest that most of the studies about abscission were carried out in the model plant *Arabidopsis* and have focused on flower abscission. These results also indicated that this topic was extensively studied in tomato, citrus, sweet pepper, litchi, and *Lupinus*. Most of these studies were achieved on tomato crops followed by sweet peppers. Regarding plant growth regulators (PGRs), ethylene has the highest frequency, followed by auxins and abscisic acid (Fig. 2).

A similar search within the *Capsicum* genus, which included the keywords “*Capsicum annuum*,” “bell pepper,” “pepper,” “abscission,” and “ethylene,” indicated several studies on bell pepper, abscission, and ethylene, in the second and third most important, respectively; *Capsicum frutescens* was also present, although with less importance (Fig. 3).

This review article focuses on the abscission process in plants, integrating the advances carried out up to date to comprehend this phenomenon. The abscission of fruits and flowers of bell pepper, because of its great importance for the crop, is emphasized.

distinct stages. Initially, the abscission zone is formed, followed by the activation of abscission signaling. Subsequently, enzymatic hydrolysis of the middle lamella within the abscission zone occurs, leading finally to elongation and increased volume of the AZ cells. And fourth, the abscission protective layer differentiates and completely seals the separated cell layers [18,19].

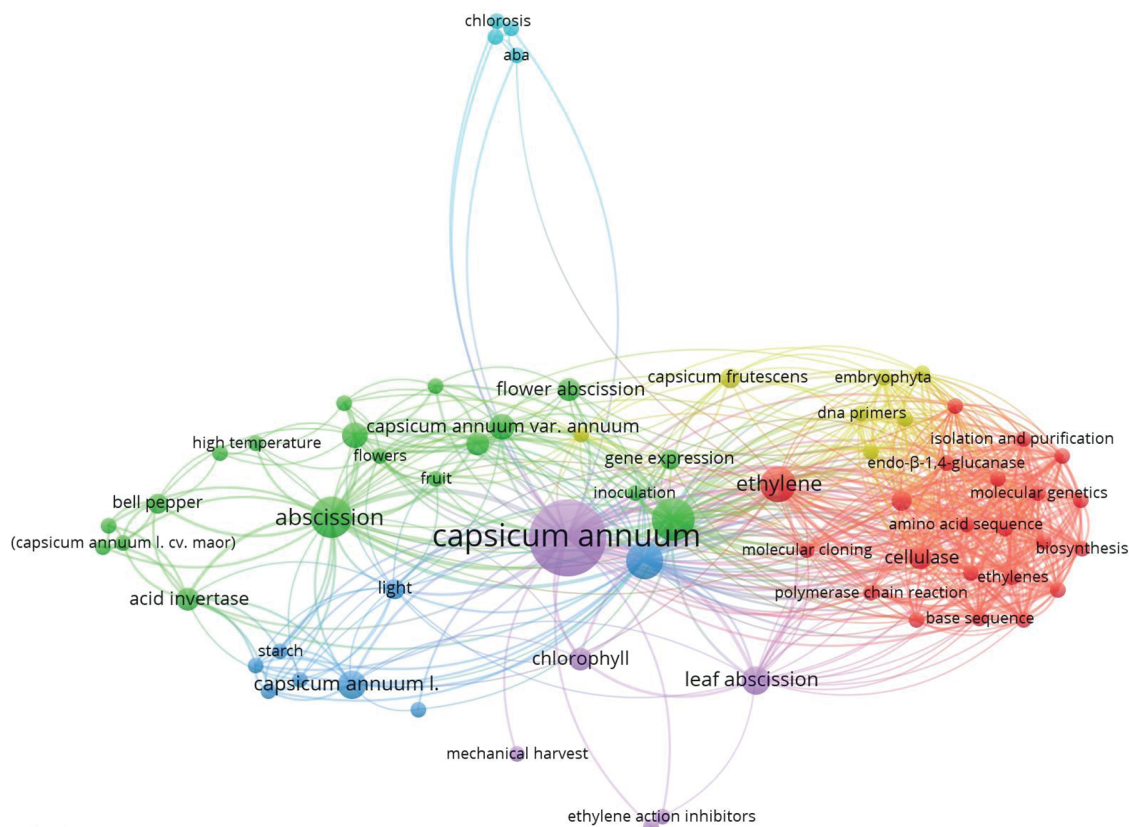


Figure 3: VOSviewer frequency of co-occurrence keywords taking into account two as the minimum number of occurrences of a keyword, from 1972 to 2024. Based on the scientific platform Scopus[®], with reference to the following keywords: *abscission/capsicum*. 73 keywords in 6 groups were taken into consideration; the largest group is made up of 42 elements

In agriculture, the control of abscission is vital as it affects yield and crop quality [20]. In some crops, abscission can have relevant yield implications. For example, in litchi plants, abscission may occur in approximately 95% of flowers, causing less than 5% to reach fruit maturity. Similarly, in bell peppers, between 67% and 81% of fruitlets are aborted. Abscission also affects quality and post-harvest storage in some crops [21,22].

2.1 *Abscission Zone*

The abscission process occurs in a specific cell area, named the abscission zone (AZ). The AZ is often band-shaped and develops at the beginning of organ development [23]. The cells within the AZ typically exhibit a smaller size compared to the surrounding cells and contain densely packed cytoplasm. Additionally, within the AZ, the bonds of the cell wall are separated in the middle lamella (the pectin layer responsible for joining adjacent cells) [23]. Once the abscission process starts, cells in the AZ

expand, and the middle lamella is dissolved by hydrolytic enzymes, which allows cell separation. Thus, a new protective epidermic layer may grow to protect exposed cells at the abscission location [24].

Recent advances in genetic, molecular, and biochemical methods have brought about a better understanding of separation process. Besides PGRs, additional molecules (IDA peptide, hydrogen peroxide) that play a crucial role in events during abscission were identified [25].

The initiation of the AZ development, which may eventually lead to abscission, commences during the early stages of organ development. Certain genetic aspects of floral organ AZ development in Arabidopsis have indicated the necessity of the *BLADE-ON-PETIOLE 1/2 (BOP1/2)* transcription factors for its formation [26]. The homeodomain transcription factor *BREVIPEDICELLUS (BP)* serves to prevent excessive enlargement of the AZ in floral organs of Arabidopsis [27], while the MYB transcription factor *ASYMMETRIC LEAVES1 (ASI)* is responsible for establishing the positioning of the AZ in floral organs [28]. The *A. thaliana Homeobox Gene1 (ATH1)*, a BELL-type transcription factor, is essential for the location and development of the stamen AZ [29]. In tomato plants, a MADS-domain transcription factor, such as *JOINTLESS*, is necessary for the formation of the pedicel AZ [30,31]. Even though the MADS-domain transcription factors regulate the activation of abscission in Arabidopsis, it has not been demonstrated that they regulate the development of floral organ or leaf AZ [32,33].

The mechanisms governing the initiation of abscission signaling have been predominantly elucidated in the model plant, Arabidopsis. The signaling events during the activation phase of abscission commence with the expression of enzymes that modify the cell wall, leading to the dissolution of the pectin-rich middle lamella of the AZ. In Arabidopsis, the mutant of Inflorescence Deficient in Abscission (IDA) fails to undergo abscission, and its AZ cannot be differentiated [34]. However, it is probable that the signaling elements involved in the initiation stage of abscission also contribute to the ultimate formation of the protective layer within the AZ [34]. For example, the overexpression of IDA, a gene essential for abscission initiation, leads to excessive scar differentiation in the AZ.

The AZ in yellow lupine flowers (*Lupinus luteus*) has a particularly active transcriptional network at specific stages, as reflected by the expression profile of *LIBOP* [35]. Transcripts of *LIBOP* were detected in the cytoplasm and nucleus of the cell AZ. After abscission, cells AZ accumulate reactive oxidative species and are stimulated by an increasing quantity of uridine-rich small nuclear RNA, along with a heightened synthesis of poly(A) mRNA. *LIBOP* plays the role of a mobile key regulator for abscission.

2.2 Advances in Flower and Fruit Abscission

The research on the plant-abscission process has focused mainly on fruit crops, including litchi (*Litchi chinensis*), mango (*Mangifera indica*), citrus crops, grapes (*Vitis vinifera*), apple (*Malus domestica*) and peach (*Prunus persica*); fruiting vegetables, mainly tomato (*Solanum lycopersicum*); and the Arabidopsis plant (*Arabidopsis thaliana*). These studies have permitted the identification of genes, peptides, and PGRs involved in the entire process (Table 1) [36].

Table 1: Recent advances on plant abscission

Species	Studied organ	Abscission cause or factor	Reference
<i>Solanum lycopersicum</i>	Flowers	Carbohydrate starvation	[37]
<i>Lupinus luteus</i>	Flowers	Drought jasmonate	[38]
<i>Litchi chinensis</i>	Fruits	<i>LcKNATI</i>	[39]
<i>Lupinus luteus</i>	Flowers	Drought	[40]

(Continued)

Table 1 (continued)			
Species	Studied organ	Abscission cause or factor	Reference
<i>Solanum lycopersicum</i>	Flowers	<i>SIIDL6</i>	[10]
<i>Mangifera indica</i>	Flowers, fruits	<i>MiIDA1, MiIDA2</i>	[41]
<i>Solanum lycopersicum</i>	Fruits	Suppression of <i>SIBL4</i>	[42]
<i>Litchi chinensis</i>	Fruits	Brassinosteroids	[43]
<i>Solanum lycopersicum</i>	Petiole	Ethylene, hydrogen sulfide	[44]
<i>Litchi chinensis</i>	Fruits	<i>LcHSL2</i>	[45]
<i>Arabidopsis thaliana</i>	Leaves, floral organs, fruits	Drought	[8]
<i>Litchi chinensis</i>	Flowers	<i>LcIDL1</i>	[22]
<i>Arabidopsis thaliana</i>	Flowers	IDA MAPK	[46]
<i>Euphorbia pulcherrima</i> and <i>Pisum sativum</i>	Flowers	Decapitation	[47]
<i>Arabidopsis thaliana</i>	Floral organs	<i>AGL15</i>	[33]
<i>Vitis vinifera</i>	Inflorescences	Gibberellic acid, shade	[48]
<i>Malus X domestica</i>	Fruits	Cold stress	[49]
<i>Malus domestica</i>	Fruits	Thinning, Abscissic acid	[50]
<i>Prunus persica</i>	Flowers, fruits	Ethylene, <i>PpIRL1</i>	[51]
<i>Solanum lycopersicum</i>	Pedicel	Auxins, ethylene	[31]
<i>Arabidopsis thaliana</i> and <i>Citrus</i>	Floral organs, fruits	IDA Peptide	[52]
<i>Solanum lycopersicum</i> , <i>Diplotaxis tenuifolia</i> and <i>Arabidopsis thaliana</i>	Flower, pedicel	Alkalinization of cytosol, ethylene	[53]

In woody plants, the existing knowledge on flower and fruit abscission has focused primarily on the effects of environmental stresses, which are related to this process [13]. Many of these environmental factors alter PGR balances and/or carbohydrate metabolism (Table 1), but the precise process are not fully understood. PGRs serve as the abscission effectors, of which the equilibrium of ethylene and auxins is particularly important. The balance between photosynthesis and reserve mobilization is responsible for the intricate regulation of the carbohydrate equilibrium [6]. PGRs and carbohydrates are integral components of complex signal transduction systems, particularly during stress responses.

2.2.1 Primary and Secondary Abscission

The process of primary abscission in poinsettia (*Euphorbia pulcherrima*) inflorescences, as compared to the non-abscising wild-type pea mutant, reveals that in poinsettia, the primary abscission process initiates at the epidermis around the pedicel. As the AZ develops towards the center of the pedicel, the pedicel continues to grow through cell division and cell elongations of surrounding tissues. Subsequently, the AZ is pushed upward, resulting in the formation of a cone-shaped stump when the bud falls. This cone-shaped bud is a

characteristic feature of floral organ abscission in poinsettia. The expression of gene sequence 90a (XM_011094475/AY188755) is required for abscission; both in pea and poinsettia. These findings could have broader implications for understanding abscission, given that pea and poinsettia diverged in evolution approximately 94–98 million years ago. Consequently, any shared gene or process is likely to be widespread in the plant kingdom [47].

2.2.2 Elucidated Causes or Factors in Plant Abscission

In mango, two coding genes like the INFLORESCENCE DEFICIENT IN ABSCISSION (IDA) were isolated, the *MiIDA1*, and *MiIDA2* genes [41]. These *MiIDA-LIKE* genes were triggered by ethephon (Ethylene). The ectopic expression of both genes in Arabidopsis led to the promotion of floral organ abscission. This was accompanied by an early increase in the cytosolic pH of flower AZ cells, a phenomenon associated with abscission, and by the activation of cell separation in vestigial AZ [41]. The abscission ability was restored in an *AtIDA* mutant, with overexpression of both genes. These findings indicated that *MiIDA1* and *MiIDA2* play roles in influencing mango fruit abscission.

In litchi fruits, the external application of brassinosteroids (BRs) decreased ethylene-provoked fruit abscission by 53.75% [43]. This response was associated with reduced ethylene production and suppressed activation of the ethylene biosynthetic genes ACC-SYNTHASE *LcACS1/4* and ACC-OXIDASE *LcACO2/3* in the AZ. Two genes encoding signaling components of the BR nucleus, BRASSINAZOLE RESISTANT (BZR) transcription factors, *LcBZR1* and *LcBZR2*, were described. *LcBZR1/2* are in the nucleus and act as transcriptional repressors. These results suggest that BR suppresses abscission in ethylene-induced fruits via *LcBZR1/2*-regulated expression of genes involved in ethylene biosynthesis in litchi. The Arabidopsis *BZR1-1D* enhancement of function mutant also depicted tardy floral organ abscission at the same time with reduce expression of *ACS/ACO* genes and minimum ethylene production, so it can be inferred a conservation in Arabidopsis of mechanisms in the organ controlled by *BZR* transcriptional factors during abscission through the regulation of ethylene biosynthesis.

LcKNAT1, a cluster of *ARABIDOPSIS THALIANA-LIKE PROTEIN1 (KNAT1)*, acted as a negative regulator, controlling fruit abscission by suppressing the expression of ethylene (ET) biosynthetic genes in litchi [39]. *LcKNAT1* is capable of directly inhibiting the transcription of *LcEIL2* and *LcEIL3*, two homologs of *ETHYLENE INSENSITIVE 3-like (EIL)* in litchi, and these homologs act as positive regulators in ethylene-activated fruit abscission by directly stimulating the expression of genes responsible for ethylene biosynthesis and cell wall degradation [39]. The *LcKNAT1-LcEIL2/3* regulatory module may play a role in fruit abscission in litchi, and it is suggested that *LcKNAT1* could suppress ethylene biosynthesis and signaling to regulate fruit abscission.

The suppression of genetic expression of *BEL1-LIKE HOMEODOMAIN4 (SIBL4)* induced the elongation and abscission of fruit pedicels in tomato plants (*Solanum lycopersicum* cv. Micro-TOM) [42]. The anatomical study revealed an increased number of epidermal cell layers and the absence of a AZ in the *SIBL4* RNAi lines, as compared to the wild-type plants. RNA-seq analysis indicated that the control of abscission by *SIBL4* was linked to the modified abundance of genes associated with meristems, auxin transporters, signaling components, and cell wall metabolism. Additionally, *SIBL4* had a positive impact on the concentration of auxin in the AZ.

The *AGAMOUS-LIKE 15 (AGL15)* was recognized as a potential regulator of HAE expression and governs a portion of the mechanisms and regulatory networks involved in a receptor-mediated signaling pathway that manages of the floral organ abscission [54]. The overexpression of *AGL15* led to reduced expression of HAE and a delayed abscission phenotype. Studies using chromatin immunoprecipitation indicated that *AGL15* binds to the HAE promoter in floral receptacles. Furthermore, *AGL15* undergoes differential phosphorylation during floral receptacle development in a manner dependent on mitogen-

activated protein kinase-kinase 4/5. The phosphorylation of *AGL15* by MAP kinase is crucial for the complete expression of HAE, thus completing a positive feedback loop controlling HAE expression [54].

The signaling mediated by the IDA peptide regulates the flower abscission induced by low light in tomato plants (*Solanum lycopersicum*) [10]. The patterns of expression for an IDA-like gene (*SIIDL6*) were examined using tandem mass spectrometry to detect and characterize the mature *SIIDL6* peptide. Knockout lines of *SIIDL6* exhibited flower drop, and the application of *SIIDL6* peptide hastened abscission. Overexpression of *SIIDL6* rescued the IDA mutant phenotype in Arabidopsis, indicating functional conservation across species. *SIIDL6*-mediated abscission occurred through an ethylene-independent pathway. Additionally, a regulatory module involving *SIWRKY17* and *SIIDL6*, which operates under low light conditions, induced abscission by upregulating the expression of enzymes related to the remodeling and disassembly of cell walls.

In *Nicotiana attenuate*, the *JASMONATE ZIM DOMAIN* (*NaJAZd*) protein counteracts flower abscission [55]. The mutant that does not express *NaJAZd* (*arJAZd*) displays a higher rate of flower abscission, perhaps through regulation of jasmonic acid (JA), jasmonoyl-L-isoleucine tiers and/or expression of *NaMYB305* gene in flowers. This insight into the role of JAZ proteins in flower and seed development underscores the diverse functions of jasmonates and JAZ proteins.

Naturally, drop flower rate increased in 63.1% in untreated ‘Thompson Seedless’ grapevine (*Vitis vinifera*), to 83% and 99% following the application of gibberellic acid (GAc) and shading treatments, respectively [33]. Both treatments exerted a wide-ranging impact on the metabolic processes of the flower clusters. Distinct effects of shade encompassed the inhibition of photosynthesis, linked nutritional strain, imbalance in carbon/nitrogen levels, and suppression of cell division. Conversely, GAc application stimulated energetic metabolism alongside the initiation of nucleotide biosynthesis and carbon metabolism, revealing alternative pathways for abscission regulation.

In yellow lupine (*Lupinus luteus*), a water-holding capacity of 25% reduced the number of nodules in the root and stimulated floral abortion [40]. The response of the flower AZ to drought involves the increased expression of genes responsible for extensins, galactans, arabins, xylogalacturonan, and xyloglucans.

Soil water deficits leads to lipid peroxidation in yellow lupine and the increased expression of phospholipase D and lipoxygenase; concurrently, there is a substantial accumulation of JA in the AZ tissue [38]. Crucial processes in JA coupling and signaling under adverse conditions were clarified by assessing the levels and tissue-specific distribution of enzyme-providing *JASMONATE RESISTANT1* (*JAR1*) derivatives and the *CORONATINE INSENSITIVE1* (*COI1*) receptor. Simultaneously, the stimulation of AZ during flower abscission under drought conditions is intricately linked to lipid alterations, resulting in the production of JA, its conjugation, and the initiation of signaling pathways.

In ‘Hongro’ apple grafted onto ‘M9’ rootstocks under cold-stress conditions (4°C), the initiation of abscission was observed, accompanied by the increased expression of genes involved in abscisic acid biosynthesis (*MdNCED1*) and metabolism (*MdCYP707A*), as well as genes for ethylene biosynthesis (*MdACS1*) and receptor (*MdETR2*) in the pedicel [49]. For ‘Golden Delicious’ apple benzyladenine and metamitron use of application led to a 66% and 91% increase in total fruitlet abscission, respectively [50]. Additionally, the initiation of the abscission process at the cortex level is regulated by a complex network of interactions involving hormones (primarily abscisic acid and ethylene) and other signaling molecules.

In peach, the *PpILR1* enzyme, an IAA-amido acid hydrolase, directly controls the expression of *PpACS1*, which is a crucial factor in ethylene biosynthesis during fruit abscission [51]. *PpILR1* triggers the ethylene biosynthesis pathway through two mechanisms: firstly, by directly stimulating the expression of *PpACS1* via its transcriptional induction activity, and secondly, by releasing active IAA from auxin-

amino acid conjugates, thereby inducing the expression of *PpACS1* through the auxin signal transduction pathway.

2.2.3 IDA/IDL-HAE/HSL2 Pathway

The *LcIDLI* gene of litchi, a homolog of IDA, was identified and it has a comparable function to *AtIDA*, which is controlling floral organ abscission in Arabidopsis [22]. A HAESA-LIKE homolog, *LcHSL2*, was isolated and is probably engaged in fruit abscission in litchi, as well [45]. Misplaced expression of *LcHSL2* in wild-type Arabidopsis did not affect floral abscission. Nevertheless, the presence of *LcHSL2* in the *hae hsl2* mutant background completely restored the deficiency in floral organ abscission. *LcHSL2* is situated in the cell membrane, and this gene is expressed at the pedicel AZ in litchi and the floral AZ in Arabidopsis. Real-time PCR analysis revealed an increase in *LcHSL2* expression during ethephon-induced fruitlet abscission. These observations indicate that *HSL2* homologs exhibit functional conservation in both Arabidopsis and litchi, with *LcHSL2* potentially playing a crucial role in regulating fruit abscission in litchi.

Floral organ abscission in Arabidopsis is controlled by a signaling pathway that includes the peptide ligand IDA, the *RECEPTOR-LIKE KINASES (RLKs)* HAE and *HSL2*, and a downstream MAP KINASE (MAPK) cascade [46]. The SERK family *RLKs* act in a redundant way in controlling floral organ abscission downriver of IDA and upriver of MAPK cascade. IDA induces the formation of heterodimers between HAE/HSL2 and SERKs, leading to reciprocal transphosphorylation. Notably, the interaction of SERK3 residues with the immune receptor *FLS2* is regulated, and the involvement of the brassinosteroid receptor *BRI1* is essential for the IDA-regulated HAE/HSL2-SERK3 interaction. This suggests that SERKs act as co-receptors of HAE/HSL2 in sensing.

It was proposed that the IDA–HAE–HSL2 complex contributes to a pathway for abscission that is not dependent on ethylene [56], based on results of no abscise flower organs in the *ida* mutant ethylene-treated. IDA-HAE/HSL2 signaling is critical as a signal inducer for the conclude organ abscission and it is preserved in many species, but it is not participate in initiating the abscission processes of floral organs in the AZ and it controls later stages of the process, in particular the ethylene promotes the *IDA* gene in the AZ flower organs in Arabidopsis [57].

2.2.4 Tomato Abscission

The initial differentiation of pedicel AZ in tomato plants occurs when the sepal differentiates from the floral primordium. The AZ cells are formed in the internal region of pedicel and gradually extend to the external tissues. Cells in the AZ surrounding the vascular tissue and cortex can divide, so that, the AZ has a capacity like meristems [58].

Normally, abscission occurs when ovule-fertilization unsuccessful, or after the fruit totally matures. To study the process of pedicel absorption, it is artificially induced with the ethylene-external application and by removing flowers. The initial phase of cell separation for abscission occurs in the cortex, specifically on the distal side of the AZ, when ethylene is applied to the pedicel. In the case of pedicel abscission induced by emasculation, first takes place in the epidermis AZ. The dissolution of the middle lamina is a common response to both types of abscission induction. Essential components such as cell wall hydrolysis enzymes and remodeling proteins, including polygalacturonase (*TOMATO ABSCISSION-ASSOCIATED POLYGALACTURONASE; TAPG*), endo- β -1,4-glucanase (*CELLULASE; CEL*), *XYLOGLUCAN ENDOTRANSGLUCOSYLASE/HYDROLASE (XTH)*, and expansins, play a crucial role in the abscission process. Additionally, the enlargement of epidermal cells is stimulated to provide mechanical force and facilitate abscission. Furthermore, the formation of a thickened and lignified cell wall on the abscissa surface of the proximal side suggests the development of a protective layer to prevent pathogen invasion [31].

In this, the MADS-BOX *JOINTLESS* (*j*), *MACROCALYX* (*MC*) and *SIMBP21* genes are co-expressed in vascular tissue for the development of the AZ [31].

When the AZ cells of the pedicel of tomato sense an abscission stimulation signal, their adhesion begins to deteriorate, since genes for cell wall hydrolysis enzymes (*TAPG* and *Cel*) are expressed and components that regulate adhesion specifically increase and intensify programmed cell death in AZ [59].

Transcriptomic analysis at the onset of abscission indicated that many genes may be responsible for abscission regulatory functions, such as genes for families of transcription factors *ARF*, *Aux/IAA*, *AGL*, *KNOX*, *WRKY*, *HAT*, *AP2b*, *HLH*, and *NAC*, genes for elements of signal transduction pathways like *LRR-RLK*, a Ser/Thr protein kinase, and a component gene of an RNA-induced silencing complex, *AGO1* [60].

The tomato transcription factors, homologues of *WUSCHEL* (*LeWUS*), *GOBLET* (*GOB*), *LATERAL SUPPRESSOR* (*Ls*), and *BLIND* (*Bl*), play an important role in AZ, since they promote the maintenance of undifferentiated cells of the AZ [61].

The ERF transcription factor *SIERF52* in tomato serves as a component of a signaling pathway for pedicel abscission and plays an essential role in stimulating the expression of responsible genes for cell wall hydrolysis [62]. Additionally, the transcription factor *KD1*, a member of the *KNOTTED1-LIKE HOMEODOMAIN* (*KNOX*) family, regulates abscission by controlling genes that modulate auxin levels in tomato [63].

The *SIIDL6* gene, IDA-like, controls low light-provoked flower abscission in tomato plants [10]. The *SIBL4* gene negatively regulates fruit pedicels abscission in tomato, due to positively exerted influence on the auxin concentration in the AZ [42].

3 Bell Pepper

The *Capsicum* genus encompasses fruits that produce carotenoids, flavonoids, alkaloids, and capsaicinoids. Carotenoids and flavonoids are responsible for the attractive colors of bell peppers ranging from green to red, and even blue and chocolate colors [64]. Capsaicinoids attribute a characteristic flavor known as pungency, which is not present in bell pepper fruits [65].

Bell peppers are globally recognized as a highly sought-after vegetable due to their rich nutritional profile, including the presence of essential vitamins (A, C, E, and K1) and antioxidants. Their vibrant color, aromatic fragrance, flavor, and crisp texture contribute significantly to their widespread popularity in various culinary preparations worldwide [66]. As a crop, the abscission of flowers and fruits of bell peppers limits its production, and make it difficult to manage, and causes variations in the pepper prices.

3.1 Flower and Fruit Abscission in Bell Pepper

In bell peppers, the floral bud, flower, and fruit abscission is considered a yield-restrictive aspect [67]. Bell peppers also exhibit variations in the fruit harvesting pattern, with periods of high production alternating with periods of reduced production [4,5]. The variations in fruit development and yield pose challenges for growers in scheduling activities and managing the production cycle, leading to price fluctuations of peppers within a given season [6].

The abscission of bell peppers is associated with periods of high yields alternating with low-production periods, failure of pollination, drought stress, reduced light intensity, PGR (ethylene, and auxins, primarily), and source-demand relations (Table 2).

The recognized causes that provoke the abortion of reproductive structures (flowers and fruits) in the cultivation of bell pepper, include; high temperatures, reduced light intensity, plant density, drought, salt

stress, production alternation, pollination failure, PGR, source-demand relationships, and fruits with high growth rate. These factors are summarized in Fig. 4.

Table 2: Published research on abscission of reproductive structures in *Capsicum annuum* L.

Studied organ	Cause or factor of abscission	Reference
Flower and fruit	Fruiting alternation	[67]
Flower and fruit	Pollination failure	[68]
Flower and fruit	Drought	[69]
Flower	Shade, ethylene, and abscission-resistant cultivars	[70]
Flower	Auxins	[71]
Flower	Shading	[72]
Fruit	Assimilates and competition-domain	[73]
Reproductive organs	Temperature, ethylene, and auxins	[74]
Flower and fruit	Auxins and competition-domain	[4]
Flower and fruit	Source-demand, plant density, shading and pruning	[5]
Flower and fruit	Source-demand	[6]
Flower and fruit	Auxins	[75]
Flower and fruit	Source-demand	[76]
Flower and fruit	Auxins	[21]

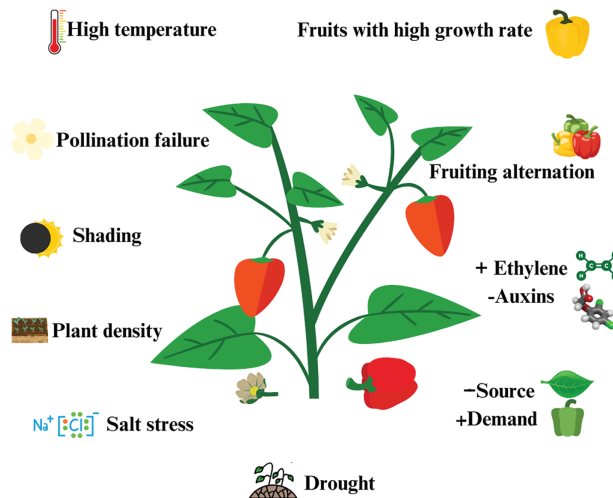


Figure 4: Causes of abscission of reproductive structures in bell pepper (*Capsicum annuum* L.)

3.1.1 Temperature

Exposure to high temperatures (32°C and 40°C) triggered the rise of abortion rate of reproductive structures in bell pepper cv. 'Maor' [74]. High temperatures were related to an increased production of ethylene and a lower concentration of IAA, which are induced in the AZ of reproductive organs.

Ethylene production was caused by the expression of genes that encode *ACS*, *ACO*, ETHYLENE RESPONSE (*ETR*, *ERS*), CONSTITUTIVE TRIPLE RESPONSE (*CTR*), and ETHYLENE INSENSITIVE3 (*EIN3*) [44]. Auxins are synthesized by the *AUXIN RESPONSE FACTOR 1/2* (*ARF1/2*, *19*) genes [77].

3.1.2 Light and Pruning

Floral abscission was also caused by reduced light intensity or leaf removal in bell peppers. These conditions decreased carbohydrate accumulation (mainly sucrose and reducing sugars) [72]. The light intensity threshold for daily carbohydrate accumulation in sink leaves was considerably lower than in flowers, resulting in higher daytime carbohydrate accumulation in the sink leaves compared to the adjacent floral buds under all light intensities. This differential accumulation indicates a competition for assimilates between these organs. Notably, bell pepper cv. ‘Maor’ and ‘899’ (sensitive to abscission) exhibited lower accumulation of soluble sugars and starch in shaded conditions compared to bell pepper cv. ‘Mazurka’ and paprika cv. ‘Lehava’ (less sensitive).

In sweet pepper cv. ‘Gialte’, far-red light (FR)-encouraged fruit abortion in non-decapitated plants (<1 fruit plant⁻¹) [78]. Notably, the removal of the apical shoot led to an increase in the number of fruits per plant (6–7 fruit plant⁻¹) under both light conditions, indicating that the presence of the apical shoot has a stimulating effect on fruit abortion. This observation suggests that the apical shoot mediates the fruit abortion stimulated by FR in pepper, as FR had no influence on fruit abortion in decapitated plants. Reduced sucrose accumulation and lower invertase activities in flowers were associated with FR-stimulated fruit abortion. Additionally, under additional far-red light conditions, increased auxin levels in shoot apices promote fruit abortion by increasing competition for assimilates between apices and flowers, thereby limiting assimilate import into flowers.

The signaling pathways of trehalose 6-phosphate (T6P) and sucrose nonfermenting-related (SnRK1) appear to play a role in adjusting metabolism to sugar starvation stress in flowers [37]. This adaptation involves the regulation of starch remobilization and interactions with 3-Indole Acetic Acid (IAA), Abscisic Acid (ABA), and ET. Continuous limitation of assimilable supply leads to starch depletion in flowers, potentially resulting in abscission.

3.1.3 Plant Growth Regulators

Ethylene in bell pepper acts as an abscission promoter, whereas auxins play an inhibitory role [69]. Similarly, the best moment within the flowering stages for the application of commercial chemical products that inhibit the abscission caused by ET is when anthesis is at 45° of petals opening. The application of commercial inhibitors (IAA) has the best inhibitory effect of abscission process [71].

The auxin-exogenous application at concentrations of 50, 100, 150, and 200 µg ml⁻¹ IAA helped to improve the characteristics of growth and fruiting under high-temperature conditions in the hybrid ‘Indra’ [21]. IAA applications enhanced chlorophyll, carotenoids, carbohydrates, protein, and proline contents, reduced lipid peroxidation, and decreased cellulase activity in the pedicel of flowers of treated plants (17.15% less with 100 µg ml⁻¹ of IAA). These effects lead to a reduction in floral abortion. Similarly, there was a greater pollen viability and percentage of fruit production at high temperatures, which is equivalent to a higher yield (1.6 kg plant with 100 µg ml⁻¹ of IAA) compared to control.

The PGR successfully tested in the cultivation of sweet pepper is 4-chlorophenoxyacetic acid (4-CPA), a synthetic pesticide alike to auxin [75]. The application of 2000 ppm resulted in a higher quantity of flowers and fruits, representing a 24.50% increase in the specific cultivar ‘BARI Misti morich-1’ and 26.02% in the cultivar ‘BARI Misti morich-1’ Lamuyo, in comparison to control plants that only exhibited a 18%.

Differences, between cultivars (‘McIlhenny Select’ and ‘HP’) of *Capsicum frutescens*, regarding abscission time of deflowered pedicel, with (complete prevention of abscission for the ‘HP’ cultivar and

only 6% for the 'McIlhenny Select' cultivar) and without (abscission at 84 h for 'McIlhenny Select' and 48 h for 'HP') the application of auxins (1-naphthaleneacetic acid) in the pedicel AZ, were observed [79].

3.1.4 Nutrition

Abscission of bell pepper flowers was higher at low levels of nitrate. For instance, when 4 milliequivalents per liter (meq L^{-1}) of nitrates were supplied in comparison to the application of 9 and 14 meq L^{-1} nitrates. These results indicated a strong correlation between growth parameters and carbon or nitrogen content in plants, which is decreased when the supply of nitrates was lower [80].

A gradual rise in the concentration of total nitrogen (N), in progressive physiological stages, from 3 to 6 and 9 mM, augmented the number of flower and fruit set, and produced the greatest fruit yield ($3444 \text{ g plant}^{-1}$). This happens when $\text{NH}_4\text{-N}$ was 30% of the total (6 mM) during the vegetative phase, and $\text{NO}_3\text{-N}$ was the only source of N during the fruit filling period [81].

3.1.5 Source-Demand Relations

The abortion rate of flowers and fruits in bell peppers increased linearly as photosynthates availability decreased [73]. Practices that reduced photosynthate availability include pruning of unfolded leaves, high-plant densities, and reduction of solar radiation for a seven-day periods. Similarly, the existence of fruits of early formation in the first nodes (fruits with a high growth rate) triggered the flowers and fruits abortion. The period of greater susceptibility to abortion is from just before anthesis to about two weeks after anthesis.

The demand strength for vegetative structures tended to be lower in large-fruited cultivars compared to small-fruited ones. As fruit size increased, there was greater variability in fruiting and fruit yield. Large-fruited cultivars necessitated a higher ratio of resources to demand for fruiting, leading to an increased demand for photo-assimilates. Various methods were employed to reduce the heterogeneity of fruiting, such as enhancing the strength of the source, reducing the strength of vegetative demand, adjusting the source-demand relationship for fruit set, and controlling the rate of flower appearance. Additionally, individual fruits were harvested before reaching full maturity to achieve a reduction in fruiting heterogeneity [6].

3.2 Regulation of Abscission in Bell Pepper

Current published research on abscission in bell pepper addresses only the factors that induce or influence abscission, but the genetic, hormonal, and signaling regulatory mechanisms have not been elucidated. The advances made in the abscission process in model plants and species taxonomically related to the bell pepper are presented [82]. Further research is required since it could be different in *Capsicum*-plant species.

A model for the regulation of flower and fruit abscission in bell pepper has not fully been established. The model proposed for tomato could be used as a starting point due to the taxonomic and morphological proximity to bell pepper plants.

4 Conclusions and Future Outlooks

To our knowledge, there is no published research that fully describes the mechanisms, genes, signaling, PGR, and compounds involved in the flower and fruit abscission in bell peppers.

The genetic, biochemical, molecular, physiological, and phytohormonal factors that intervene in the abscission of reproductive organs were described in the model plant *Arabidopsis thaliana*. Mainly, in the identification of genes that take part in the abscission (*IDA*, *IDL*, *KNATd*, *RLK*, *MAPK*, *AGL15*), and it is regulated by the interaction of peptide hormone IDA, a pair of redundant receptor-like protein kinases, HAESA (HAE) and HAESA-LIKE2 (HSL2), and co-receptors of Somatic Embryogenesis Receptor-Like

Kinase (SERK). In this sense, there have been important advances, such as the identification of orthologous genes for tomato (*SIIDL6*, *SIBL4*), mango (*MiIDA1*, *MiIDA2*) and litchi (*LcKNAT1*, *LcHSL2*, *LcIDL1*). Nonetheless, the functionality of the signaling module for any other species has not been demonstrated yet. It would be pertinent and appropriate to extend and carry out the mentioned studies also for non-model plants of global economic importance, such as the bell pepper. In the same way, it would be very important to identify each of the factors that cause the abortion of flowers and fruits within the plant and the cultivation system. If these goals are achieved, the bell pepper-fruit abscission process will be effortlessly controlled under growing conditions, increasing harvesting and yield.

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