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Fruit drop in cotton: some causes

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Abstract

Various aspects of fruit abscission in cotton have been reviewed in the past. Recent advances in this field thus permit consolidation of review of the current research. A major concern among cotton growers is heavy fruit drop, that leads to direct yield loss, which occurs at the expense of squares and young bolls. Shedding of fruiting forms in cotton is the combined consequence of plant itself like hormonal imbalance, plant nutritional status, age relation, and environmental stresses like water deficit, waterlogging, high temperature, dim light, salinity, insects and diseases. These stresses result in prominent signaling modifications like hormonal imbalance. Ethylene is claimed to play a key role in abscission apparently by activating the production of cell wall degrading enzymes such as cellulases and polygalacturonase. The premature dropping of fruiting bodies can significantly increase due to these environmental stresses, which result in severe loss in cotton yield. This article is focused on both internal and external factors that leads to fruit abscission, mechanism of fruit abscission at the physiological, hormonal, and molecular level and trying to point out the missing links on different aspects of plant hormones and environmental stresses regarding fruit abscission. This article also focused on the missing pieces of the very complicated puzzle of fruit abscission process in cotton and elucidation of the mechanism by which plants perceive abscission signals and trigger phytohormone-mediated signal transduction cascades is crucial to devise fruit shedding related breeding and transgenic approaches.

Keywords: Environmental Stresses, Hormonal Imbalance, Fruit Abscission, Climate Change

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Introduction

Cotton (*Gossypium hirsutum* L.) is one of the major cultivated species for fiber around the world and regarded as the most important cash crop (Ali, 2015; Constable & Bange, 2015; Singh, 2017). Cotton for a long time fascinates the attention of agricultural scientists because of its economic importance around the world and one of the mainstays of the global economy. In term of foreign exchange and employment, cotton plays a pivotal role in the national economy of Pakistan with 0.8% share in GDP. Statistics show that cotton was cultivated on an area of 2.373 million hectares and production was 9.861 million bales during 2018–19 (GOP, 2019). A decline of 31.5 % against the target of 14.4 million bales and a 17.5 % decline over the previous 11.964 million bales production. However, this decline in cotton production is due to both abiotic and biotic stress (GOP, 2019).

Cotton production has been threatened by biotic and abiotic stresses during its entire growing season (Zafar et al., 2018). Some multiple strategies have been proposed to improve its yield and production in major cotton production regions of the world. Development of cotton germplasm lines and elite breeding material with reduced boll shedding in response to environmental vagaries has been considered an option to enhance cotton yield (Heitholt et al., 1993). The shedding of floral buds and young bolls in cotton culture has been considered major setback for its yield around the globe. Historically, it was major concern for the breeders and cotton growers, and breeders have used selection criterion such as boll retention node to select genotypes to enhance yield under stress environment. Boll abscission was considered as waste of metabolic energy and photosynthates that the plant could use more efficiently to enhance its reproductive biomass (Millhollon, 1961). A loss of 65–70 % has been estimated in form of squares and young bolls (Baloch et al., 2000). The potential of cotton fruiting was high, if breeding lines with the lowest habit of fruit shedding may be developed. A major challenge among the breeders was to develop cotton ideotypes with the potential to produce high fruiting bodies but with intact fruits for several fold increase in yield potential of the cotton plant. In this regard, cotton plant nutritionist and physiologist have developed chemical or management practice that saves the fruiting bodies from shedding. However, understanding of the plant physiology, molecular and genetic mechanisms involved in the boll shedding may further help plant breeders and geneticist to develop new cotton breeding lines with greater success. Therefore, this review article is written with the aim for providing better understanding of the mechanism underlying the fruit drop in cotton plant.

Fruit shedding related theories

Two theories have been emerged in previous studies to explain the fruit shedding process, nutritional theory and the hormonal theory (Addicott & Lynch, 1955; Guinn, 1982a; Jordan, 1983). According to nutritional theory, internal competition among plant parts leads to a deficiency of carbohydrates toward the developing fruit that results in fruit abscission (Ehlig & LeMert, 1973; Guinn, 1982a; Mason, 1922). The hormonal theory is purely based on phytohormones like auxin, ethylene, abscisic acid, cytokinin, gibberellins. Ethylene and abscisic acid are the abscissions promoting hormones while auxin is abscission inhibiting hormone whereas cytokinin and gibberellins have variable effects. Young bolls contain a high concentration of abscission promoting hormones then the older

one which contains less concentration and vice versa, with the concept that the bolls are susceptible to abscission is age-dependent (Davis & Addicott, 1972; Guinn, 1982a; Rodgers, 1980).

Abscission zone formation/abscission layer

Abscission zone (AZ) is a developmentally defined region of cells which is mediated by cellular processes that consequently leads toward organ separation (Addicott, 1982; Lewis et al., 2006; Taylor & Whitelaw, 2001). Abscission process occur in the cells that lie in the abscission zone. The cell wall degrading enzymes are secreted that digest the middle lamella and loosen the cell wall (Brummell et al., 1999; Goldental-Cohen et al., 2017; Guinn, 1998), resulting in the drop off of a fruit or leave. Normally abscission usually progresses through the peduncle transversely; the square and young boll drop, with the prominent scar left on the fruiting branch. However, in some situations, the abscission zone may occur at an oblique angle, sometimes the squares and young bolls may dry and hang on the plant (Dutt, 1928; Lloyd, 1920). During the stage of pedicel development, anatomical studies shows the formation of abscission zone and characterized by several dense and small layers of cytoplasmic cells in inactive form, until abscission promoting signals perceived by the cells occurs through phytohormone imbalance (Estornell et al., 2013; Frankowski et al., 2015b).

Mechanism of fruit shedding

The shedding process is initiated by the formation of the abscission layer between fruiting forms and plants (Lewis et al., 2006; Taylor & Whitelaw, 2001). Thus, due to heavy fruit weight, the peduncle becomes weak and fruiting organ abscise. Abscission process is divided into three distinct phases. The first phase is the signaling phase, in which plants receive signals via development (pollination, senescence/cutout) or environment (biotic and abiotic) and abscission zone formation takes place. The regulatory phase is the second phase, which is characterized by hormonal imbalance mediated abscission through AZ cells dissolution this is sensitive to ethylene and ABA and insensitive to auxin, and the third phase is considered as the final phase, in which abscission related transcription factors and genes activate which enhance the level of cell wall degrading enzymes like cellulases and polygalacturonases consequently dissolution of the middle lamella and organ separation takes place (Tripathi et al., 2008). ETR: ethylene response, ACO: 1-aminocyclopropane-1-carboxylic acid oxidase, ACS: 1-aminocyclopropane-1-carboxylic acid synthase, ARF: auxin response factors (Fig. 1).

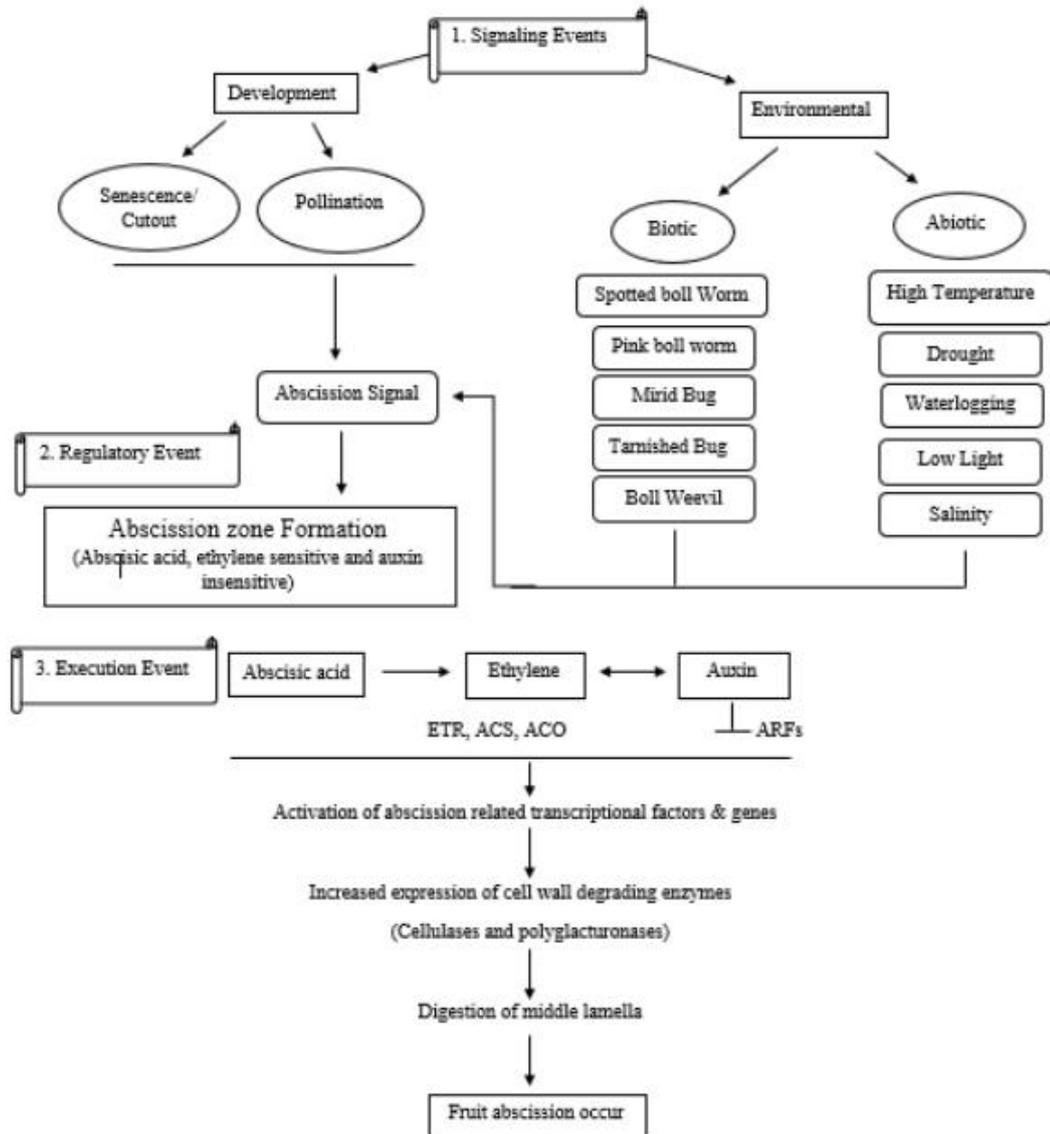


Figure 1. Hypothetical model of fruit abscission in cotton adapted from (adapted from Sawicki et al., 2015; Tripathi et al., 2008).

Factors affecting fruit shedding in plants

1. Hormonal Control

Plant growth regulators are referred as the signaling molecules produced by the plant under varying climatic conditions. Plant growth regulators fluctuate in response to various biotic or abiotic. The fluctuations in the level of different phytohormones are the plant response which leads to changes in gene expression involved mainly in their biosynthesis and regulations. Phytohormones are crucial in every aspect of plant biology, it is a fact that large numbers of fruit regulating genes are a part of hormone biosynthetic and signaling pathways (Xie et al., 2013). Plant hormones act as a remote controller in the abscission process, but they are highly dependent on environmental conditions. Any sudden change in optimum conditions leads to hormonal imbalance, which ultimately results in detrimental effects on the growth and development of the plant. Therefore, it was very crucial to understand the exact mechanism of hormonal changes during cotton fruit drop. There are some hormones which were regulating in the complex process of fruit abortion including auxins, ethylene and abscisic acid

Table 1. Role of plant hormone in abscission

Phytohormone	Effect on abscission	References
Auxin	————*	(Patel, 1993)
Ethylene	+++	(Bonghi et al., 2000)
Abscisic acid	+++	(Vakma, 1976)
Cytokinin	————	(Rodgers, 1981b)
Gibberellins		(Varma, 1976)

Where, ———— indicate inhibition, +++++ indicate promotion

a. Auxins

Auxin is regarded as a versatile plant growth regulator with diverse developmental and environmental responses including organ abscission and senescence controlling (Sauer et al., 2013; Ellis et al., 2005). Studies were conducted including various exogenous exposure of auxin and auxin analogs to find out their role in the abscission process. There are many studies that indicated that auxin have its pivotal role in the abscission process (Patel, 1993). Indole –3– acetic acid (IAA) and naphthalene acetic acid (NAA) proved to have inhibitory effect on abscission process (Addicott & Lynch, 1955), but it triggered abscission process when applied on the proximal side of the abscission zone. This theory reflects the significance of the relative auxin concentration rather absolute concentration. (Addicott et al., 1955; Rubinstein & Leopold, 1963). The theory also explains that auxin plays both triggering or inhibiting role on abscission process depending upon the timings and area of exposure. Therefore, auxin inhibits abscission as long as it moves towards the abscission zone (AZ) when distally applied. It was inducing abscission when proximally applied due to auxin incapability from moving towards AZ and ethylene effect was more prominent by proximal exposure of auxin (Abeles, 1967). Also, abscission depends upon the tissue sensitivity and insensitivity to ethylene (ETH). Two conditions happening in auxin-mediated abscission process. During the first condition before excision/decapitation, auxin inhibits abscission because the tissue is comparatively insensitive to ETH. In contrast, the tissue becomes sensitive to ETH immediately after excision/decapitation during the second condition. Auxin is likely to

delay the first condition. Although, auxin unable to inhibit abscission during the second condition and somehow promote the abscission because the tissue soon become sensitive to ETH. This promotion and inhibition of abscission, the time–conditional effects of auxins explained by Leopold, 1971. The precise mechanism by which auxin repress abscission is still not clear by the enormous studies. However, abscission triggering enzymes such as cellulases being suppressed by the auxin application (Ratner et al., 1969; Abeles, 1969). Another mechanism seems by auxin is to improve selective permeability and cell membrane integrity, consequently, it may avoid the production of cell wall degrading enzymes like cellulase, pectinase which ultimately stop the dissolution of the middle lamella of the cell wall. Although there is still no evidence of this hypothesis (Sacher, 1957). Abscission related gene expressions can be blocked by auxins in Arabidopsis (Noh and Amasino (1999); Tucker et al. (2002)). This is the contemporary accepted model of auxin–mediated execution of the abscission process (Dhanalakshmi et al., 2003; Meir et al., 2006; Meir et al., 2010). In short, auxin depletion by any factor, which disturb the movement of auxin in the AZ leads to the ethylene sensitivity in the AZ. Strongly inhibitory action shown by IAA; indeed, it is universally involved in abscission inhibition. However, auxin may also have a promotive effect under certain experimental conditions (Addicott & Wiatr, 1977).

b. Ethylene

Normally the concentration of ethylene in plants is low, its concentration is enhanced by different biotic and abiotic clues and especially during the abscission process (Lin et al., 2009). In the early 1950s role of ethylene as a dominant regulator of abscission was unknown. Nowadays, it is well established that ethylene is the key player in abscission promotion. Recent work indicates that during the period of young fruit abscission, the abscising fruit produces almost 4 times more ethylene than the retained fruit. It is reported that 1–2 days before the fruit abscission, ethylene was produced by the abscising fruit which was about 3.0–5.7 ul/kg h. In contrast, the retained fruit produces less than 1.0 ul kg⁻¹ h (Lipe & Morgan, 1973b). It was concluded that optimum concentration of ethylene production is 0.033 ul fruit⁻¹. The wall of abscising cotton fruit produces 0.052 ul fruit⁻¹ h, which is approximately 50% more than the normal fruit (Lipe & Morgan, 1973a). These studies claimed that ethylene had regulatory role in cotton fruit abscission. For instance, the results of research conducted on many plant species such as olive (Weis et al., 1988) and apple (Kolarič et al., 2011) showed a significant role of ethylene as a dominant promoter of abscission. Moreover, it was found that a 3–fold increase in ethylene production before abscission in cotton (Morgan et al., 1992). The most commonly used fruit dropping agent is ethephon (2–chloro ethyl–phosphonic acid) which was widely used for promoting fruit abscission in many crop species including cotton (Guo et al., 2018; Zhu et al., 2010). Two action–mechanism of ethylene are well documented: (a) slow down the transport and enhance abolishing of auxins (Beyer & Morgan, 1971) and (b) activate the synthesis of cellulase and pectinase in the abscission zone (Abeles & Leather, 1971; Abeles, 1969; Ratner et al., 1969; Riov, 1974) (Fig. 2). It was reported that movement of auxins was slow down by ethylene which leads to auxins depletion and tissue sensitivity to ethylene (Beyer & Morgan, 1971; Morgan & Gausman, 1966). However, hindrance in the way of auxin transport leads toward auxin depletion and this ultimately results in organ abscission (Morgan & Durham, 1975). In contrast to auxins, both the action–mechanism

of ethylene promotes abscission. A second most important function of ethylene is to activate the synthesis of cellulase (Abeles, 1969; Reid et al., 1971; Ratner et al., 1969) and polygalacturonase (Riov, 1974) in the abscission zone. While ethylene not only activates cellulase synthesis but also promotes the secretion of these enzymes which deteriorate the middle lamella and cell walls of cells in AZ (Abeles & Leather, 1971; Roberts et al., 2000; Taylor & Whitelaw, 2001; VAN Doorn, 2002; Zhu et al., 2010). This cell wall hydrolysis in AZ initiate by the ethylene signals (Morgan et al., 1992). The whole mechanism of abscission, final effects shown by ethylene were potent for dropping. Hydrolytic enzymes were responsible for walls loosening and cell separation in AZ where ethylene activates the transcription of genes that are encoding these hydrolytic enzymes (Bonghi et al., 2000). Previous studies have shown that ethylene mediated leaf abscission in cotton results in higher activity of ethylene biosynthesis and cellulase enzymes which is more than 5-fold and 2.7-fold respectively (Mishra et al., 2008). Similarly, different abscission promoting defoliant were applied to petiole of the cotton leaf which results in approximately twice the expression of *GhACS* and *GhCELI* (Du et al., 2014). Finally, the influence of ethylene was essentially promotive in the fruit abscission process due to its highly volatile nature (Addicott & Wiatr, 1977).

The balance between these two antagonistic hormones is important because it acts as divergent co-regulators in the abscission process. The function of auxin is to inhibit the abscission process while ethylene causes the abscission process. between the both, which remains dominant perform its function well in the abscission zone.

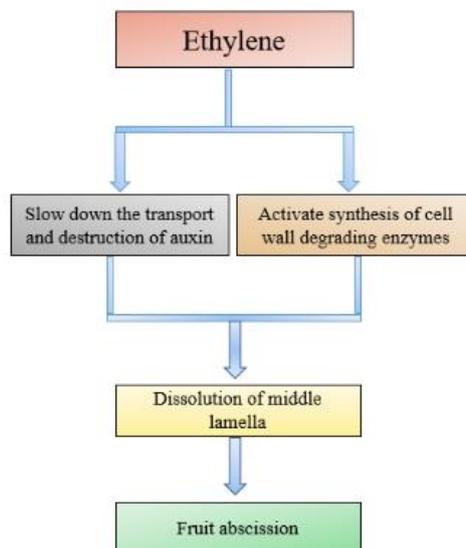


Figure 2. The possible role of ethylene in the abscission process. Two mechanisms of action exist for ethylene that causes fruit abscission.

Ethylene biosynthesis pathway

In higher plants, the ethylene biosynthesis pathway has been well established. Evolution of ethylene from methionine via S-adenosyl-L-methionine (SAM) and 1-aminocyclopropane-1-carboxylic acid. There are two main steps devoted in ethylene biosynthesis, one is the conversion of SAM to ACC and the second step is ACC to ethylene, which is catalyzed by ACC synthase (ACS) and ACC oxidase (ACO) respectively (Yang et al., 2015). Two ethylene biosynthetic genes ACS (ACC synthase gene) and ACO (ACC oxidase gene) are well known for many years. It belongs to the multigene family, and some members of this family are involved in fruit abscission. For instance, in cotton, one ACS gene i.e., GhACS (Du et al., 2014) and one ACO gene i.e., GhACO (Mishra et al., 2008) have been significantly expressed during abscission. Furthermore, in apple four ACO genes i.e., MdACO1, MdACO2, MdACO3, MdACO4 (Wiersma et al., 2007), and five ACS genes i.e., MdACS1, MdACS2, MdACS3, MdACS5A, MdACS5B transcript has been isolated and characterized (Cin et al., 2005). These results indicated that ethylene biosynthetic genes were responsible for fruit abscission and should be precisely controlled by abscission related signals.

c. Abscisic Acid

In the early 1960s, **Abscisic Acid** (ABA) was the only compound isolated from the cotton fruit, identified during fruit abscission mechanism by Addicot and colleagues (Ohkuma et al., 1963). It was believed that compound was involved in abscission, so it was called as abscisic acid (Addicot et al., 1968). Further studies changed this concept in fact, nowadays it is known that ABA has an indirect effect which is mainly driven by ethylene. Like ethylene, ABA also induce organ abscission by slowing and disrupting the basipetal movement of IAA in the AZ (Chang & Jacobs, 1973) because of stimulating ethylene production and cellulase activity in AZ (Craker & Abeles, 1969) which ultimately leads toward organ abscission (Varma, 1976; Tariq et al., 2017). For instance, abscisic acid (ABA) content were high in abscising boll than the intact bolls, suggesting that exogenous application of ABA either to intact bud/boll or boll explant induced their shedding (Vakma, 1976) (Fig. 3). However, there was more involvement of ABA in regulating fruit abscission rather than leaf abscission (Milborrow, 1974). For instance, level of ABA was found to be increased during organ abscission in the many crop species including Hibiscus (Swanson et al., 1975), orange (Sagee & Erner, 1991), *Lupinus luteus* (Porter, 1977), *Malus domestica* (Vernieri et al., 1992), mandarins (Zacarias et al., 1995), and cotton (Suttle & Hultstrand, 1993). In addition, the inhibitor of ABA biosynthesis Norflurazon (NFZ) reversed the stimulatory effect of ethylene during cotyledon abscission in *G. hirsutum* L. (Suttle & Hultstrand, 1993). However, mechanism of ABA and ethylene control needs to be explored in detail.

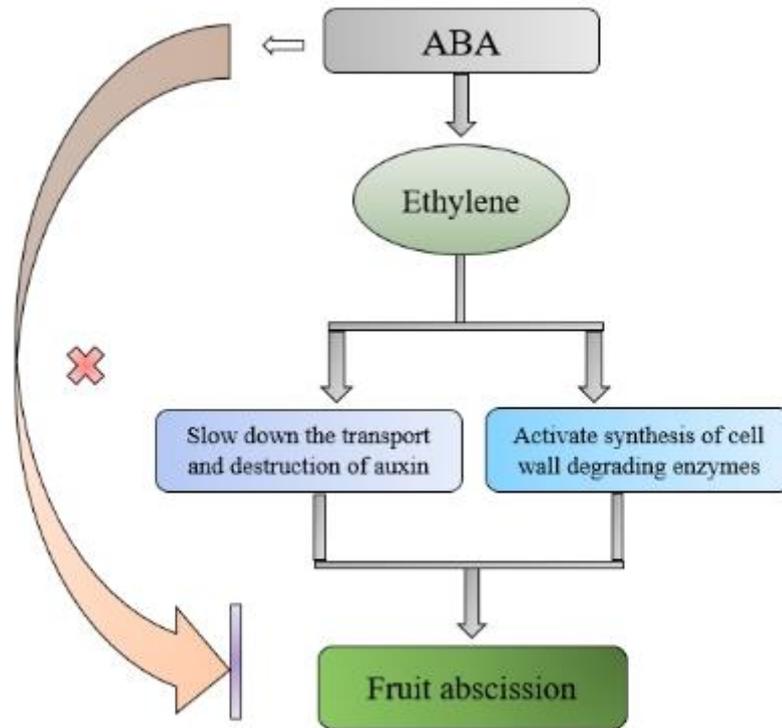


Figure 3. Role of Abscisic Acid in Abscission process

d. Cytokinin

In the abscission process, the role of cytokinin appears to be indirect. Some time it inhibits or promotes abscission, depending on the site of application and time (Addicott, 1970). Cytokinin provides the ability of an organ for metabolite competition which delay or prevent senescence (Letham, 1971). Therefore, senescence enhance the sensitivity of an organ to ethylene mediated abscission promoting effects (Leopold, 1971). Varma (1967a) showed the promotion of boll abscission by treatment of cytokinin, despite those which directly applied to the abscission zone, which results in a decrease in boll shedding. Furthermore, Rodgers (1981b) quantify the activity of cytokinins in the abscised and retain boll. At the 7 and 10 days following anthesis, the abscised boll contains less concentration of cytokinin activity, while a higher concentration of cytokinin activity was observed in retain boll.

e. Gibberellins

Gibberellins concentration also have effects on abscission process. Some studies showed the promotive effects of gibberellins to abscission (Chatterjee, 1977; Varma, 1976) and conversely, inhibit abscission (Bhardwaj et al., 1975; Varma, 1976). When gibberellic acid was applied to the intact fruit of cotton it inhibits abscission. In contrast, when applied to cotton explant it promotes abscission. In the first case, gibberellins inhibit abscission by facilitating the mobilization of nutrients to that fruit that leads to enhancing fruit retention (Addicott, 1970). In other words, intact fruits treated with gibberellin inhibit the abscission while untreated fruit of the same plant leads to abscise (Walhood, 1957).. , Most studies conclude that GA retards abscission by increasing fruit retention rate (Walhood, 1957; Bhardwaj et al., 1975. It is evident that gibberellin contents high in retained fruit and low in abscising fruit (Cognee, 1975). Another study concluded that maximum gibberellin activity was found in cotton fruit during the critical stage of fruit shedding (Rodgers, 1980). In addition to the major hormones, other hormones like jasmonic acid, brassinosteroid, and salicylic acid also play a pivotal role in fruit abscission in other crops. However, their function in cotton fruit abscission is relatively less characterized.

f. Plant nutritional status

A large amount of sugars is required for fruit production and there is a strong source and sink relationship that exists but with increasing boll load, nutritional (carbohydrate) deficiency enhances the rate of fruit shedding. Many studies indicated that nutritional deficiency causes fruit shedding. Complete removal of plant leaves causes 100 percent fruit abscission and partial removal of leaves enhances the rate of fruit shedding but not 100 percent shedding of fruit (Eaton & Egle, 1954; Johnson & Addicott, 1967). Low light is another factor of nutritional deficiency and causes fruit shedding by limiting the photosynthesis (Guinn et al., 1981). There is an inverse relation of carbohydrate contents of leaf sap and osmotic pressure with fruit abscission. When carbohydrate demand exceeds the supply, fruit abscission rate enhances (Hearn, 1972). Any factor which decreases the plant's nutritional status results in the increased rate of ethylene production (Guinn, 1976a), and ethylene is potent for fruit abscission.

g. Role of cell wall degrading Enzymes

Cell wall degradation is considered as the crucial and limiting factor in fruit abscission mechanism. In the AZ cell wall composing components like cellulose and pectins must be decomposed before fruit abscission. Usually, abscission precedes by the enzymatic dissolution of primary walls of cells and middle lamella in the abscission zone (Webster, 1973). Two enzymes are well documented: cellulase and pectinase, which digest the middle lamella and soften the cell walls of cells in the abscission zone, contribute to weakening the peduncle (Webster, 1973; Riov, 1974). Plasmalemma is the site of synthesis of these enzymes while the middle lamella and primary cell wall is the site of action of these enzymes (Addicott & Wiatr, 1977). These are characterized by increased enzyme activity and gene expression of cell wall hydrolytic enzymes. Cellulases and polyglacturonases are two main enzymes implicated in the abscission process in several species including cotton and are directly regulated by ethylene (Li et al., 2010; Du et al., 2014). However, following enzymes are reported to be more crucial for this mechanism:

i . Cellulases

In most plant species including cotton, cellulase activity enhances before abscission (Abeles et al., 2012; Ratner et al., 1969). Previous studies have shown that ethylene mediated leaf abscission in cotton results in higher activity of ethylene biosynthesis and cellulase enzymes which is more than 5-fold and 2.7-fold respectively (Mishra et al., 2008). Furthermore, different abscission promoting defoliant were applied to petiole of the cotton leaf which results in approximately twice the expression of *GhACS* and *GhCELL1* (Du et al., 2014). Ethylene was found to be essential for the secretion of cellulase enzymes (Abeles and Leather, 1971).

ii: Polyglacturonases

In the middle lamella, insoluble pectates, mainly calcium pectates are hydrolyzed to pectic acid. Usually, abscission precedes by the increased pectinase activity in the abscission zone (Riov, 1974). But no effect was shown by pectinesterase in the abscission zone (Moline et al., 1972; Ratner et al., 1969). However, pectinase activity may be sufficient to cause abscission (Morre, 1968). Furthermore, different abscission promoting defoliant were applied to petiole of the cotton leaf which results in the elevated transcript of *GhPG* (Du et al., 2014)

iii: Transcriptional regulation in abscission zone (AZ)

The architecture of a plant is consistently being shaped and reshaped due to the congregation and alteration of cell wall components consistent notably of celluloses, pectins, hemicelluloses, lignin, and structural proteins. The basis of development in the plant as well as response to the environment is maintained by the restructuring of these cell wall components. Architects of a plant have a dynamic nature of fruit abscission as well as reproductive development that involves changes in the structure and function of the cell wall. Abscission zone is a developmentally defined region of cells which is mediated by cellular processes that consequently leads toward organ separation (Addicot 1982).

The scientist has studied the abscission process for more than 170 years. The role of ethylene and auxin in the abscission process has been found nearly 100 years and more than 50 years respectively. Until now, scientists demonstrated all the classical plant hormones (auxin, cytokinins, ethylene, abscisic acid, gibberellins, jasmonic acids, and brassinosteroid) which are affecting the timing of abscission. In recent years, many signaling components are found in-addition to above including different transcriptional factors, MAP kinases, receptor-like kinases, a small signaling peptide, and membrane traffic regulators be censorious in differing phases of abscission process. In response to developmental and environmental clues gene expression regulation by transcriptional factors (TFs) is the key mechanism that control changes in AZ at cellular level. A study shows different abscission specific TFs in soyabean lea abscission like MYB, WRKY, AP2 IAA (Kim et al., 2016). Another study revealed that transcriptional factors like (Blade on petiole) BOPs were involve in differentiation of abscission zone in *Nicotiana tabacum* and *Arabidopsis thaliana*. (Hepworth et al., 2005; McKim et al., 2008; Wu et al., 2012), Furthermore, a study concluded that ethylene and ABA mediated flower abscission in *L. luteus* results in more expression of BOP homologue (*LIBOP*) (Frankowski et al., 2015a). However, their function in cotton fruit abscission is relatively less characterized.

iv. Reactive oxygen species (ROS)

Reactive oxygen species (ROS) including superoxide, singlet oxygen, hydroxyl radical, and the hydrogen peroxide are the byproducts of different environmental stresses (Sakamoto et al., 2008b; Waqas et al. 2021). ROS accumulation occurs under environmental stresses which leads to detrimental changes in the cellular components like proteins, lipids and nucleic acids (Xu et al., 2019; Zafar et al. 2020). A study concluded that ROS plays a regularity role in cassava leaf abscission as ROS accumulation is observed in the site of abscission zone (Liao et al., 2016). Another study concluded that there was no connection of ROS in the fruit abscission zone of olive, but promoted abscission in the leaf abscission zone through altering oxidative stress by ethephon treatment (Goldental–Cohen et al., 2017). Similarly, ROS–mediated leaf senescence was also observed in rice which is accompanied by chloroplast damage (Zafar et al. 2021). An *in vitro* abscission analysis revealed that hydrogen peroxide was associated with ethylene and has role in leaf abscission (Sakamoto et al., 2008a). Previous studies show that fruit abscission occurs due to carbohydrate deficiency. For instance, longan fruit abscission occurs due to nutritional stress which may be mediated by ROS (Goldental–Cohen et al., 2017). However, their function in cotton fruit abscission is relatively less characterized.

2. Environmental Factors that causing fruit shedding

Any environmental factor that interferes with the expression of genotypic potential is known as stress. Stresses comprise of both biotic and abiotic. Cotton drop fruit for a variety of reasons, apparently by affecting the hormonal balance which in turn enhances ethylene and activates hydrolytic enzymes responsible for fruit abscission. Here are some important causes of shedding which have been identified are listed below: Square and boll shedding enhance by several environmental factors like high temperature, water deficit, waterlogging, salinity, low light, inorganic nutrients, fruit age, thick plant stand, insect and diseases (Guinn, 1982a; Tariq et al., 2017). Fruit shedding prevails even though no insect and disease infestation is indicating the more contribution of abiotic stresses in this mechanism (Cook, 1921). Role of various abiotic stress for fruit abscission has been discussed in below listed subsection of the review.

a. Water Stress

Water is one of the main environmental factors which affect cotton fruit shedding in both conditions either water deficit or surpluse water (Guinn, 1982a). In water deficit condition, the cotton plant is unable to regulate its temperature through evaporative cooling. Secondly, prolonged water deficit causes premature leaf shedding which results in fewer photosynthates supply toward the developing fruit and finally results in fruit shedding. For instance, in the case of water deficit, the rate of boll shedding is enhanced correspondingly as water potential of leaf decrease from -10 to -24 bars. The age of tissue is important while inducing abscission by water stress. The bolls which retain 14 days post–anthesis (DPA) are less prone to shed under severe water stress, while squares and immature bolls are more sensitive to minor water stress. Bolls of less than 2cm diameter were more prone to shed as the water potential of leaf decreases below -1.9 MPa (McMichael et al., 1973). Water stress indirectly caused fruit abortion by enhancing ethylene evolution in the abscising boll of cotton (Guinn, 1976b). The water deficit

partially increases the ABA content of bud but increased the ABA contents of the flower as far as 66%. However, the effect of water deficit on immature boll abortion might trigger by changes in ABA but not from the alteration in IAA (Guinn et al., 1990). In water deficit, squares were more prone to shed before the flowering stage (McMichael, 1979). Similarly, young squares with the age of 1 week after appearance were more prone to shed (Ungar et al., 1989). Squares and flowers show enhance ABA contents when imposed on water deficit (Guinn et al., 1990) as well as bolls (Guinn and Brummett, 1987). Water stress indirectly caused fruit abortion by enhancing ethylene evolution in the abscising boll of cotton (Guinn, 1976b) and a decrease in IAA contents of cotton bolls (Guinn and Brummett, 1987).

Excessive water content (waterlogging) also prove to be a major constraint to yield losses in many parts of the world including Pakistan (Crosson & Anderson, 1992). In the case of waterlogging, the level of oxygen in soils decreased that caused stomatal closure, resulting in reduced CO₂ fixation and photosynthate supply, causing fruit shedding. In cotton roots, deficiency of oxygen triggers the biosynthesis of ethylene precursor (ACC) and this ACC move towards the stem and converted into ethylene (Christianson et al., 2010). For instance, plentiful water results in fruit shedding, particularly in heavy soil due to poor aeration of roots (Longenecker & Erie, 1968). This poor root aeration signals ethylene production by 1-ACC in shoots where it is converted in ethylene and enhances shedding (Bradford & Yang, 1980). Similarly, another study concluded that ethylene biosynthesis is involved in fruit shedding in waterlogged conditions and this yield loss by fruit shedding can be ameliorated by using anti-ethylene agents like aminoethoxyvinylglycine (AVG) (Najeeb et al., 2015). Furthermore, ABA biosynthesis genes (CcNCED3) expressed in the citrus plant under water stress conditions and level of ABA in roots increases (Agustí et al., 2007; Gómez-Cadenas et al. 1996) which in turn stimulate the activity of ACC synthase in roots. This ACC remains in roots and not move towards shoots due to water stress. After rehydration, restoration of water flow moves ACC from roots to leaves where this ACC metabolizes to ethylene which in turn triggers leaf abscission (Tudela & Primo-Millo, 1992).

b. High temperature

Cotton is relatively heat tolerant among many C₃ plants. However, excessive-high temperature leads to square and young boll shedding which consequently results in yield losses (Dunlap, 1945; Powell, 1969; Zafar et al., 2018). Square and boll shedding is enhanced by extremely high temperatures (Powell, 1969) and ultraviolet radiation (Zhao et al., 2005). Similarly, the cotton yield is negatively affected by high temperatures due to immense fruit shedding (Reddy et al., 1992; Zafar et al., 2018). Three aspects seem by high temperature mediated square and young boll shedding. 1) High-temperature results in reduced fruit set, pollen sterility, square shedding, and boll shedding (Song et al., 2015). Fruit shedding under heat stress is due to reproductive failure and carbohydrate supply inhibition (Najeeb et al., 2017). 2) High temperature enhances the rate of dark respiration (Guinn, 1974) and photorespiration thereby consuming the available photosynthates which result in nutritional stress (Guinn, 1976a). Young cotton bolls enhance ethylene evolution when facing nutritional stress (Guinn, 1976a). 3) It is reported that ABA, ethylene, and cell wall degrading enzymes such as cellulase and pectinase induced by high temperature

during the reproductive stage and results in fruiting forms abscission (Echer et al., 2014; Tariq et al., 2017) (Table 2).

Table 2. Optimum temperature ranges for the processes related to fruit development

Plant reproductive processes	Optimum temperature (°C)	References
Maximum fruiting efficiency	30 – 40°C	(Hodges et al., 1993)
Photosynthesis efficiency decline	>35°C	(Bibi et al., 2008)
Chlorophyll contents decline	38/20°C	(Snider et al., 2009)
Membrane integrity decline	>35°C	(Bibi et al., 2008)
Membrane integrity decline	>35°C	(Bibi et al., 2008)
Respiration rate enhance	30/28°C	(Loka and Oosterhuis, 2010)
Pollen germination	28 – 37°C	(Burke et al., 2004)
Pollen tube growth	28–32°C	(Burke et al., 2004)
Poor fertilization efficiency	38/20°C	(Snider et al., 2009)
Immature boll shedding	>32°C	(Reddy et al., 1996)
Complete fruit shedding	40/32 °C	(Hodges et al., 1993)

c. Light

Sunlight is essential for the cotton plant to produce photosynthates in the process of photosynthesis. It is reported that square and boll shedding enhance during the period of low light intensity (Sorour & Rassoul, 1974). This low light accomplishes by high plant population, cloudy weather, and excessive vegetative growth (Tariq et al., 2017). Any condition that increases the leaf area index (LAI) can increase mutual shading which decreases the light intensity in the canopy. For instance, leaf size increase by the excess of nitrogen and abundant moisture (Boyer, 1976). Furthermore, an increase in LAI and mutual shading is mediated by the high plant population. Another study concluded that as the plant population increases the total number of fruiting decrease particularly in the lower portion and shedding increase (Brown, 1971). Furthermore, it is reported that a combination of abundant moisture, high plant population, and excess nitrogen enhances vegetative growth and consequently results in fruit shedding with marked yield reduction. Results of (Gerard et al., 1976a; Gerard et al., 1976b; Gerard and Reeves Jr, 1974; Gerard and Reeves, 1975) concluded that crowding of plants decreases the light intensity which leads to decrease in fruiting initiation rate and retention of already formed fruit. Notably, fruit shedding occurs due to nutritional stress as the intensity of low light decreases photosynthesis and ultimately less production of photosynthates toward developing fruit forms (Goodman, 1955). Similarly, low light-mediated fruit abscission is mainly due to

enhance ethylene evolution in fruiting organs (Guinn, 1976a). Enhancement in ethylene evolution consequently results in fruit shedding.

d. Salinity

Among all field crops cotton is considered as most salt tolerant. However, excessive salts in the soil or irrigated water leads toward yield reduction. Salinity is another factor that received little attention concerning fruit shedding. The reason may be restricting or precise control of the soluble salts in the root zones, outdoor under natural environmental conditions. The salts present in the soil as well as in irrigated water in varying concentrations and proportions, in the form of sulfates and chloride of sodium magnesium and calcium (Longenecker, 1973). For instance, the study concluded that the application of 100 mg l⁻¹ of chloride and 200 mg l⁻¹ of sulfate causes yield reduction by 39 and 43% respectively (Eaton, 1955).

d. Deficiency of inorganic nutrients

Inorganic nutrients deficiency leads to fruit shedding, by reducing in photosynthetic rate, by reducing the translocation of photosynthates or by directly affecting the synthesis of hormones. The nutrient elements deficiency causes the fruit shedding (Guinn, 1976a).

i. Nitrogen

Plant of cotton requires a relatively large amount of nitrogen than other elements for maximum yield. In the soil, nitrate is not fixed unlike phosphate and potash, and therefore, readily leaches from the root zone. In the soil, the only lasting form of nitrogen is provided by organic matters, but unfortunately, a large amount of soil is depleted by organic matters due to warm conditions of cotton-growing areas. Therefore, nitrogen is required in the soil for maximum yield. The deficiency of nitrogen may enhance the ABA contents in leaves (Goldbach et al., 1975; Radin & Ackerson, 1981). Furthermore, nitrogen is required for photosynthesis (Nevins & Loomis, 1970) and is a constituent of IAA and cytokinins. Therefore, deficiency in nitrogen results in fruit shedding (Addicott, 1973). It was found that minimum boll shedding was observed with a high rate of nitrogen, results in the maximum number of bolls and highest yield (Reddy and Rao, 1970). Despite this, excessive nitrogen level also causes fruit abscission. For instance, it was found that a high level of nitrogen significantly lowers the bolls number, boll retention rate, and boll weight (Zhang et al., 2011). Furthermore, deficiency of nitrogen causes premature fruit shedding consequently lint yield is affected (Cetin et al., 2018). Another study was conducted to evaluate the fruit shedding and yield in three cotton varieties i.e. CIM 499, CIM 511, CIM 707 for varying nitrogen rates from 50 to 200 kg per hectare and concluded that fruit shedding decreases with 50 to 150 kg per hectare (Dar and Khan, 2004). Additionally, for fruit retention, a nitrogen rate of @150 kg per hectare is considered as optimum (Khan & Dar, 2006).

ii. Zinc

Zinc deficiency also causes fruit shedding by limiting photosynthesis and also zinc is required for IAA synthesis (Skoog, 1940; Tsui, 1948). because IAA is the major hormone that inhibits the process of abscission. Zinc deficiency also reduces leaf per unit area photosynthesis (Ohki, 1976), and consequently leaves become smaller (Hewitt, 1963). Furthermore, carbonic anhydrase is an enzyme that plays a significant role in photosynthesis, and zinc is the main component of this enzyme.

iii: Boron

The boron deficiency causes shedding of squares and young bolls in cotton (Lancaster et al., 1962). Boron mediated fruit shedding is accomplished by the effect on the translocation of sugars (Eaton, 1955). For instance, a mild deficiency of boron may not slow down the vegetative growth instead of producing rank growth which consequently results in lower boll setting (Hinkle, 1968). For instance, a study concluded that the application of boron does not affect fruit production, fruit retention, and yield as compared to control (Heitholt, 1994). Boron is required for vigorous phloem and sugar transport. In contrast, it was concluded that the application of boron @ 15kg per hectare is effective on the reproductive part and reduces the shedding rate by 7.3 percent as compared to control (Abid et al., 2007).

iv: Calcium

In the cotton deficiency of calcium causes fruit shedding and suggested the role of calcium in the middle lamella (Calcium pectates) as a possible reason (Addicott, 1973; Addicott and Lynch, 1955). It was found that severe Ca deficiency causes complete failure in boll setting by affecting the translocation of carbohydrates (Joham, 1957). In addition, a deficiency of Ca decreases the movement of auxin towards the abscission zone (Dela Fuente and Leopold, 1973). Restriction in auxin transport toward the abscission zone leads to abscission promotion.

Biotic Stress on Fruit Abscission

Fruit shedding is not only attributed to insects, but diseases also cause the fruit to drop. Disease injury may be of two types; one is direct via causing infection to fruit or boll rotting and second is indirectly first leaves defoliation subsequent fruit shedding occurs (Guinn, 1982a). Table 3 illustrate the type and nature of various diseases that lead to fruit shedding (**Table 3**)

Table 3. Types and nature of various diseases lead to fruit shedding

Name		Damaged Type	Reference
Bacterial <i>Xanthomonas</i> <i>malvacearum</i>	Blight	Directly	(Brinkerhoff, 1970)
Verticillium <i>Verticillium albo-atrum</i>	Wilt	Indirectly	(Presley, 1953)
Fusarium <i>Fusarium oxysporum</i>	Wilt	Indirectly	(Smith, 1953b)
Anthracnose <i>Glomerella gossypii</i>	boll rot	Directly	(Smith, 1953a)
Leaf <i>Ascochyta gossypii</i>	Spots	Indirectly	(Blank, 1953)

Possible remedies to control fruit abscission in cotton

It was concluded that cotton plant had inherent capacity to shed bolls in response to photosynthates starvation triggered by hormonal changes. Some environmental stresses enhance the rate of flower or boll shedding. The accelerated shedding rate. can be controlled to some extent by adopting the following possible remedies:

Girdling is the technique to girdle the stems of plants for the sake to prevent downward translocation of sugars, and fruit easily accumulate above the girdle and reduces fruit abscission to some extent. It is one of the oldest techniques to retain fruiting structures. After girdling the application of mepiquat chloride during the anthesis stage reduce fruit shedding up to 15.8% as compared to control (Xiao–man et al., 2014). However, due to the laborious nature of this technology, it is difficult to adapt on a large scale. Improving agronomic practices: 1) Proper maintenance of soil nutrition by application of balanced fertilizers. 2) Balanced irrigation to avoid water deficit and waterlogging. 3) Avoid high plant population and upright growth. 4) Adjusting the sowing date so that the peak reproductive phase must not coincide with a rainy period, high temperature, and drought. Another effective approach to prevent fruit abscission by using PGRs. A) 1–MCP ethylene antagonistic. Application of 1–MCP enhances the rate of fruit retention particularly in upper canopy (Da Costa et al., 2011). B) IAA or NAA, auxin shows the inhibitory effect on fruit abscission that's why the application of naphthalene acetic acid (NAA) @10 ppm reduces the fruit shedding by 18 percent (Patel, 1993). Moreover, the application of the above compounds regulating ethylene production or blocking its actions or biosynthesis pathway which reduces fruit shedding. Furthermore, the application of boron @ 15kg per hectare is effective on the reproductive part and reduces the shedding rate by 7.3 percent as compared to control (Abid et al., 2007).

Future perspectives

Hormones play a key role in deciding the abscission of fruit and have been studied extensively, but it remains a challenge to identify their receptors and signaling components relevant to fruit abscission in cotton. The fruit abscission mechanism is complex and multiple. Nevertheless, there is still a need to isolate and analyze a large number of genes involved in this process. To unravel or facilitate the fruit abscission mechanism by using promoters that regulate fruit abscission related gene expression under specific developmental or external stimuli. The elucidate mechanism by which plants perceive abscission signals and trigger phytohormone–mediated signal transduction cascades is crucial to devise fruit shedding related breeding and transgenic approaches.

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