



SHEDDING OF FRUITING STRUCTURES IN COTTON: FACTORS, COMPENSATION AND PREVENTION¹

[DESPRENDIMIENTO DE ESTRUCTURAS DE FRUTA EN ALGODÓN: FACTORES, COMPENSACIÓN Y PREVENCIÓN]

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SUMMARY

The fruiting potential of advanced cotton cultivars is not a limiting factor for achieving yield targets but retention of squares and flowers for successful maturation into bolls is major challenge. In this article, we focused on why shedding occurs, its mechanism, yield losses, plant self-compensation, effects on plant growth and possible management to ameliorate its adverse effects. We concluded that it is quite unfair to blame single factor, instead it is an integrated effect of plant and stress factors i.e., high temperature, drought, thick plant stand, insects and diseases etc. contribute to accelerate shedding which ranges about 40-50%. The stresses induce the excessive production of degrading enzymes like pectinase, cellulose and hydrolase, while ethylene and abscisic acid is produced excessively to hasten the degradation process for shedding. The physiological disturbance contributes 7-35 and 42-64% abscission of unopened flowers and bolls, respectively. The square and flower are more frequent to shedding at high temperature compared to immature bolls. The flowers and boll shedding up to 30% is tolerable limit because cotton can recover yield provided weather support the crop later in season. The self-regulated abscission of floral parts is not easy to control under field conditions, however, the adverse effects of stress mediated shedding can be ameliorated with girdling and avoiding pest and stressful conditions, application of plant growth regulator (PGR) to control vegetative growth and abscisic acid (abscission promoter) and ethylene inhibitors like naphthalene acetic acid, silver thiosulfate and 1-methylcyclopropene.

Keywords: auto-regulation; compensatory mechanism; yield loss; management.

RESUMEN

El potencial fructífero de los cultivares avanzados de algodón no es un factor limitante para lograr objetivos de rendimiento, pero la retención de cuadrados y flores para una maduración exitosa en las cápsulas es un reto importante. En este artículo, nos centramos en por qué se produce el derramamiento, su mecanismo, las pérdidas de rendimiento, la autocompensación de la planta, los efectos sobre el crecimiento de las plantas y la posible gestión para mejorar sus efectos adversos. Concluimos que es bastante injusto culpar a un solo factor, en cambio es un efecto integrado de la planta y los factores de estrés, es decir, la alta temperatura, la sequía, la planta gruesa, los insectos y las enfermedades, etc. contribuyen a acelerar el desprendimiento que oscila entre el 40-50%. Las tensiones inducen la producción excesiva de enzimas degradantes como pectinasa, celulosa e hidrolasa, mientras que el etileno y el ácido abscísico se producen excesivamente para acelerar el proceso de degradación para el desprendimiento. La alteración fisiológica contribuye 7-35 y 42-64% de abscisión de flores y cápsulas cerradas, respectivamente. El cuadrado y la flor son más frecuentes al derramamiento a baja temperatura en comparación con las cápsulas inmaduras. Las flores y el derramamiento de cápsulas hasta el 30% es límite tolerable porque el algodón puede recuperar la producción siempre que el clima apoye el cultivo más adelante en la temporada. La ausencia autorregulada de las partes florales no es fácil de controlar en condiciones de campo, sin embargo, los efectos

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adversos del derramamiento mediado por estrés pueden ser mejorados con el ceñido y evitar las plagas y las condiciones estresantes, la aplicación del regulador del crecimiento vegetal (PGR) para controlar el crecimiento vegetativo y ácido abscísico (promotor de abscisión) e inhibidores de etileno como ácido naftalenoacético, tiosulfato de plata y 1-metilciclopropano.

Palabras clave: Auto-regulación; Mecanismo compensatorio; pérdida de rendimiento; administración.

INTRODUCTION

Cotton is the king of fibers and is being grown in more than 76 countries all over the world (Saranga et al., 2001) with a major contribution from India (27.05%), China (22.67%), USA (13.22%), Pakistan (7.10%), Brazil (6.54%) and others (23.42%) for year 2015 (Cotistics, 2016). Its cultivation extends across five continents and covers an area of more than 30 M ha across the world. The genetic improvement in cotton had achieved the target of more fruiting but it is major challenge for cotton producer to retain these fruiting forms. The potential yield of genetically improved varieties is not fully realized due to their indeterminate growth behavior and poor boll set. The production of new reproductive structures starts at 3-4 weeks after sowing and continues with the vegetative and reproductive development. Three important events occur in cotton reproductive growth in form of appearance of squares, its opening (flowering) and maturation to bolls or shedding. The maturation of square into flowers and flowers into bolls is crucial for achieving potential yield but these are often shed before entry to next developmental stage. Therefore, the monitoring is crucial to study the shedding pattern.

Cotton crop potentially produces sufficient number of bolls but the proportion of those, which are carried to maturity is low and growers rarely harvest 25-30% of the total. The problem is more pronounced in stress conditions either from biotic or abiotic factors. In cotton, fruit drop may be up to 65% to 70% in form of squares, flowers and small bolls (Baloch et al., 2000). The shedding of fruiting bodies in various cotton cultivars ranged from 41.76 to 63.63% throughout growth season (Haneef et al., 2001). It has been estimated that 60% shedding of fruiting forms is due to over production (Oosterhuis and Jernstedt, 1999). The physiological based shedding of unopened flowers and bolls in cotton ranged from 7-35 and 42-64%, respectively (Goswami and Dayal, 1998). The abscission of squares and young bolls is self-regulatory because cotton plant is incapable of supplying food to all emerging fruiting structures in field conditions. The formation of abscission layer between plants and fruiting forms initiates the shedding process. Thus, it weakens the peduncle to support the heavy weight bolls. While, the small squares remain attached to fruiting branches.

The shedding of bolls and square in cotton is controlled by plant and environmental factors. Hence, plant developmental stage and stressful conditions determines the commencement and progress of shedding. The plant factors include hormonal balance, assimilates supply and plant nutritional status, whereas moisture, temperature and light are major environmental concerns. The article was written with the objective to seek out the plant and environmental stimuli of fruit shedding with an overview of its mechanism and management tools potent to fruit retention.

PLANT RELATED FACTORS OF SHEDDING

Relationship with age and fruiting position

The squares and bolls are vulnerable to abscission at any time during their growth but mostly the shedding occurs within a week of appearance and post-anthesis for squares and flowers, respectively (Crozat et al., 1999). The squares shedding is most common up to the formation of small bolls with age of 10-14 days because the cell wall thickening prevents the formation of abscission layer.

The tendency of shedding increased with the distance away from main stem irrespective of age of fruits. This hold true because boll at first position has double source of assimilate supply from its subtending leaves as well as from leaves at main stem. The food supply is limited to bolls away from position 1st and boll weight is continuously reduced at 2nd and 3rd position (Bednarz et al., 2005). Therefore, of the total bolls produced at first position 47 % shed, whereas at position four and five, this figure may be up to 77% (Crozat et al., 1999). The flowers at first position may shed before anthesis and on average, 30% and 23% of fruiting forms shed before and after anthesis, respectively (Heitholt, 1993). The ratio of mature bolls also varied from bottom to top node and it has been noted that 73, 24 and 2% were from 1st, 2nd and 3rd node position, respectively on main stem. The chances of retention of bolls located at first and second position on 3rd to 8th nodes on main stem may be up to 95% in optimal growth conditions. Towards the distal end of the main stem, the chances of retention of bolls located at the second position are

decreased and if retained, the size is smaller towards top.

It is the well-established fact that retention of first position boll is vital for higher yield. The bolls at first, second and third sympodial position contribute more to harvestable yield with 55.91% to 63.48%, 26.33% to 31.43% and 7.04 to 10.65%, respectively (Anjum et al., 2001). Furthermore, a major contribution in total yield is from bolls located at first and second position on 10-16 nodes (Silvertooth et al., 1999). The results from study on fruit retention and shedding pattern of BT hybrids (containing Cry IAc toxin) and their counterparts non-BT hybrids revealed that BT hybrids produce 30% less square and retained 25% more bolls in comparison with non BT plants because most of bolls are located on initial nodes which remained barren in case of non-BT plants (Hebbar et al., 2007).

Hormonal Regulation

The plant hormones actually coordinate between developmental and environmental stresses through conducting a chemical message within plant. The shedding is regulated by growth hormones and it had been classified that abscisic acid and ethylene are promoters and auxins and indole acetic acid (IAA) are inhibitors while gibberellins and cytokinins had variable effect. The abscisic acid (ABA) has double effect on shedding; it directly increases cellulase activity at abscission zone and indirectly, it hastens the ethylene production and reduces the auxin transport. The gibberellic acid (GA) is not only a promoter of shedding of buds but also inhibits the bolls drop by counteracting the effect of applied ABA, and it was confirmed that application of 100 ppm GA to flowers improved retention (Walhood, 1958).

The ethylene has been reported to have a role in induction and progression of organ shedding (Mishra et al., 2008). The ethylene weakens the cells at abscission zone by degrading the cell wall through secretion of degrading enzymes like cellulase and pectinase to hasten shedding. The concept of reduced shedding in proportionality to boll age (Section 2.1) was studied by Guinn (1982) who concluded that decrease in ethylene evolution with age was one of the hormonal factors. The most commonly used defoliant or fruit drop agent is Ethephon (2-chloroethyl phosphonic acid-ethrel) which is basically ethylene releasing compound and it had been widely used to facilitate the shedding of fruits of cotton and cherry etc. During peak production of ethylene, ABA may synergistically induce abscission (Suttle et al., 1993). Likewise, the abscission triggering effect of ABA in cotton is primarily due to its stimulatory

effect on ethylene production (Taiz and Zeiger, 2002).

The hormones exist in plants in particular proportion and any changes in this ratio may promote the shedding. The IAA inhibits and ABA promote the abscission process. Guinn and Brummett (1988) investigated the content of IAA and ABA in floral buds 9 days before and after anthesis and found that concentration of ABA increases and IAA decreases after anthesis and vice versa before anthesis and suggested the proportion very important for fruit drop. It was concluded that resistance to abscission is correlated with IAA and susceptibility with ABA content. Water deficit stress induced shedding was also explained by increasing ABA and decreasing IAA (Guinn and Brummett, 1987). These results suggested that retention of fruiting bodies was positively related with IAA and negatively with ABA concentrations at abscission zone.

EXTERNAL FACTORS/PLANT STRESSES

Nutritional Factors

A good nutritional plan is necessary to achieve the target of better yield by retaining the fruiting forms for successful development to bolls. Almost, all the essential nutrients have indirect role in shedding process and boron remains at the top in this concern. The pollen germination and pollen tube growth is basic for fertilization which is disrupted by insufficient boron availability to flowers. Therefore, the incomplete fertilized flowers rarely form bolls and mostly shed. It was also suggested that the boron availability should be continuous and if withdrawn to create deficiency, it will promote shedding (Rosolem and Costa, 2000). Abid *et al.* (2007) studied the effect of boron on reproductive components and found that shedding was reduced up to 7.30% with boron application @15 kg ha⁻¹ over control plot.

The poor and excessive nitrogen supply contributes to enhanced rate of shedding by slowing photosynthesis rate. The insufficient application produced stunted plants bearing small leaves, fewer nodes and fruiting branches and slows down photosynthesis process and over supply leads to rank growth and reduce light penetration to lower canopy. Therefore, the shedding mediated by poor carbohydrates supply can be prevented by judicious use of nitrogen. The lower lint yield is produced in nitrogen deficit plants due to high shedding (Cetin et al., 2015). The impact of nitrogen application from 50 to 200 kg ha⁻¹ in three cotton cultivars i.e CIM-499, CIM-511 and CIM-707 was evaluated with respect to shedding and seed cotton yield. It was observed that nitrogen application from 50 to 150 kg ha⁻¹ decreased the shedding (Dar and

Khan, 2004). In Pakistan, increasing nitrogen rates significantly contributed to fruit retention and 150 kg N ha⁻¹ was found to be optimum (Khan and Dar, 2006).). The potassium and phosphorus fertilization also improves boll retention (Makhdum et al., 2005; Ahmad et al., 2009).

Temperature

Temperature is probably the single climatic factor being most influential for growth and development of the crops. Cotton was originated in warmer part of the world and it has thermo tolerant mechanism by which it buffers the adverse effects of elevated temperature. There is no specific temperature at which all the growth processes proceed at the maximum (Table 1). Generally, growth rate and yield is declined above 35°C (Oosterhuis, 2002). The mean seasonal temperature of some cotton producing countries like India (North), Turkey (South-East Anatolia), Sudan (Gezira) and China (Henan) is 37.5 °C, 31.5 °C, 41.8 °C and 28.2 °C, respectively (ICAC, 2009). Unfortunately, the leading cotton production countries such as Pakistan and India etc. fall in extreme temperature zones having annual maximum summer temperature up to 45 °C. In Pakistan, the cotton cultivation is confined to Punjab and Sindh provinces where flowering period coincides midsummer having temperature up to 45 °C (Rahman et al., 2004). Its consequences appear in form of heat stress which impairs the reproductive development and yield (Bradov and Davidonis, 2000). High temperature stress occurs along with incidence of high solar radiations and water stress which together exacerbate plant damage by uplifting the canopy temperature. In the sub-continent, the commencement of rainy season, however, weakens its adverse effects. By climate change scenario, elevated temperature and drought incidence may become common. It is urgent and utmost need to develop thermotolerant varieties able to cope with high temperature even at low water supply. Leaves dissipate the adverse effects of the high temperature through transpiration which is dependent on moisture supply. Therefore, the harmful effects are increased with limited water supply and this condition reduces the photosynthetic activity. Application of irrigation during heat stress is better management operation to reduce the risk associated with high temperature.

The heat stress is divided into level I and level II depending on the canopy temperature. The level I is supposed to be attained with 28-30 °C and level II is obtained when canopy temperature exceed 30 °C for 24-h day (Brown, 2002). The level I is mild stress for

fruit shed and accompanied with subsequent fruiting slowly when stress is relieved. The level II results shedding of larger fruits when long time stress effects pertain and subsequent flowering bloom may take two weeks. The cotton can tolerate heat stress for short period subject to sufficient moisture supply (Khan et al., 2008). In the present climate change scenario, the temperature of the earth is continuously increasing which is quite alarming for crop production. The negative impacts of supra-optimal temperature on cotton from climate change may increase by increasing the intensity and severity of hot days. The elevated temperatures indirectly reduce the plant water contents through increased evaporative demand (Hall, 2001). The supra-optimal temperature imparts limitations on growth in general (Table 1) but in this review, we have major concern of fruit retention. To optimize the retention of fruiting structure, we should go through the influence of elevated temperature on key processes indirectly effects the retention and its management.

Flowering relation with elevated temperature. The reproductive stage of plants appears to be more susceptible to heat stress compared to the vegetative stage (Snider and Oosterhuis, 2011). The abscission of 3-5 days old fruit forms is common when temperature exceeds 32 °C. If early flowering coincides with optimum temperature, the chances of their successful development into boll and further boll retention are higher. In this situation, the flowers appearing later in season will not retain on the plants due to competition for food. The cotton exposure at 30 °C for 13 hours was sufficient to negatively affecting the fruit set. Every increase in day temperature above the maximum reduced the lint yield @ 110 kg ha⁻¹ (Singh et al., 2007). The yield reduction is mainly from decreased photosynthesis and higher respiration at night consume the available food assimilates. The insufficient food supply to reproductive structures activates the process of square and bolls shedding and potential yield could not be attained in such situation. The squaring and flowering processes is enhanced with increasing temperature. It is evident from the studies conducted by Hodges *et al.* (1993) who observed that a rise of 10 °C above 30 °C resulted 50% increase in reproductive sites but the crop was unable to retain at 40 °C. Therefore, the incidence of higher temperature at peak squaring and flowering cannot be useful in term of lint yield.

The elevated temperature causes fruit drop by I). Male sterility, II) Photosynthesis and assimilate partitioning III) Respiration and IV) Drought.

Table 1. Critical temperature ranges for different processes of cotton

Plant parameters/processes	Optimal Temperature (°C)	References
Leaf area, intermodal distance	27-30	Reddy <i>et al.</i> (1997)
Young bolls shedding	32	Reddy <i>et al.</i> (1996)
Pollen tube growth	28 -32	Burke <i>et al.</i> (2004)
Pollen germination	28	Burke <i>et al.</i> (2004)
Fruit efficiency	>29	Reddy <i>et al.</i> (1996)
Thermal kinetic window (TKW)	23.5-32	Burke <i>et al.</i> (1988)
Stem growth	30	Hodges <i>et al.</i> (1993)
Square and flower drop	>30	Reddy <i>et al.</i> (1992)

Male sterility. The visual symptom of pollen sterility in cotton is parrot beaked bolls growing in warmer climates. The flower shedding is the result of lack of successful fertilization due to non-availability of pollens while the immature bolls are dropped by the excessive production of pectinase and enzymes (Guinn, 1982). It is necessary to retain boll that major proportion of ovule must be fertilized. The pollens could not remain viable at higher temperature during anthesis and extension of stigma may occur. This all lead to no fertilization and square abortion. Other than high day temperature, the warmer nights are equally effective for promoting male sterility based shedding of floral structures (Warrag and Hall, 1984). The pollens become non-viable at night temperature higher than 29 °C (Powell, 1969). This type of shedding will appear 17-19 days followed by onset of 29 °C or above night temperature. The most suitable day/night temperature is 30/22 °C for growth of reproductive branches, squaring and fruiting (Reddy et al., 1992). Likewise, high temperature, the cold temperature also equally promotes the shedding process like bolls formed from anthesis at < 12°C rarely retained (Yeates et al., 2010). The flowers shedding above 35 °C is common due to inviable pollen grains where flowers fail to form bolls (Baloch et al., 2000)

Photosynthesis and assimilate partitioning. Photosynthesis, the most important plant growth processes depends on surrounding temperature. The high temperature above 35 °C is major determinant of photosynthetic process in cotton by reducing the quantum efficiency of chlorophyll material (Snider et al., 2010). It has been revealed that photosynthetic rate in Pima cotton was reduced by 22% when canopy temperature exceeds from 30-33 °C to 45 °C (Wise et al., 2004). The carbohydrates balance in reproductive tissues is of prime importance for reproductive development (Zhao et al., 2005; Snider et al., 2009) and unfortunately, the high temperature alters this balance. The elevated canopy temperature during day reduced assimilates supply to emerging floral buds

and leaf tissues respire more in hotter night at the expense of stored carbohydrates. These both conditions deprive the reproductive organs from photosynthates and in this case, the cotton will shed its youngest bolls to preserve the older one. The biomass partitioning to growing bolls was at the optimum (43%) at 30/22 °C day/night temperature and fluctuation from this temperature negatively affected the assimilate partitioning toward fruiting structures (Reddy et al., 1990). The limited supply of carbohydrates in cotton is reflected in term of increased rates of fruit and square abscission.

Higher respiration. The night temperature above 25 °C would increase respiration rate that reduced the carbohydrates availability (Oosterhuis and Bourland, 2001). The existence of night temperature above the optimal for one week has little or no effect on respiration rate but extended high temperature for two to four weeks had increased the respiration (Arevalo et al., 2004). A short exposure of cotton plants at flowering for two hours from 24 °C to 27 °C and 24 °C to 30 °C during night enhances the respiration @ 49 and 56%, respectively over control (Loka and Oosterhuis, 2010).

Light

The intercepted solar radiations differ within plant canopy where production and competition for assimilates differ within plant structures. The shading during late flowering season either from prolong clouds, excessive vegetative growth and narrow row spacing stimulates the shedding and presence of all these factors at later season lead to improved earliness. At the same time, the appearance of new leaves shaded the lower canopy and abscission from this plant portion is purely with reduced light flux density. Thus, a good yield of cotton is demanding a balance in vegetative and reproductive growth. This type of shedding is mediated by reduced carbohydrates supply. The excessive early vegetative growth in non-stressed conditions reduces retention

and leaving the lower two or three fruiting branches barren or partially fruiting.

Insect infestation

It has been showed that apart from physiological and stress factor, shedding is also accentuated from insect damage. It may be result of direct damage (feeding the fruiting structures) and indirectly by sucking the nutrients from aerial plant parts. The former is mainly resulted from plant bugs and bollworms damage and the latter is contributed by sucking insects. The physiologically mediated shedding can be differentiated from insect damage by appearance of pale colour two or three days in advance. The square formed during early squaring have more chances of survival in absence of pest attack or physical stress and probability of square shedding produced later on reduces with advancement in the time of squaring.

Different insects feeds upon vegetative structures, floral buds and fruits of different ages to fulfill the food requirement and occurrence of particular insects on fruiting structure is related to crop age.t.. For instance, the boll weevil preferably feeds on small squares which are prone to shed within 1-2 days after attack (Grigolli et al., 2012). Small buds are mostly shed by plant bugs and large buds are devastated by weevils attack and bollworms causes shedding of squares and bolls. Table 2 illustrates the extent of losses caused by various insects.

Water supply

The fruit retention capacity of cotton is related to prevailing soil moisture and it is negatively affected in either excess or deficient. Water stress does not directly cause shedding but stimulates hormonal imbalance in fruiting forms (Basal et al., 2009). The sudden incidence of water deficient stress may also result complete loss of fruiting bodies rather than mature bolls which may look like mummified dry bolls. In the beginning of drought period, the rate of

bolls shedding may be higher to adjust the boll load in accordance with moisture supply and sharply slows down. The prevalence of drought conditions for long period causes premature leaf drop and shedding of fruit bodies by unbalancing the assimilate supply and demand.

The severity of drought in term of yield reduction is based upon the stage of crops and it is more detrimental at formation of reproductive structures (Loka, 2012). It may promote flowering provided that drought is mild and relieved earlier. Moisture stress during climax flowering and fruiting, on one side results in poor fruit setting due to less fruiting site and on other hand, the retention of already set bolls is also negatively affected (Aujla et al., 2005). Hence, moisture stress at this stage is quite alarming for achieving the potential seed cotton yield. The squares often shed before flowering in water stress conditions (McMichael, 1979) and the risk may last up to period of one week from appearance (Ungar et al., 1989). Similarly, young bolls may abscise provided that water stress period coincides with first fourteen days of anthesis (McMichael et al., 1973). If relieved from drought, it may take 3 weeks to bring the flowering rate at the optimum.

The drought based shedding is explained by restricting photosynthesis via minimizing the entry of CO₂ from stomata and therefore, cannot fulfill the assimilate supply (Pettigrew, 2004) and by stimulating the synthesis of abscission promoting hormones like Ethylene (Morgan and Drew, 1997) and ABA (Ullah et al., 2017). Furthermore, it is also much important to explain that distribution of carbohydrates from adjacent leaves to fruiting structure is not affected by drought as carbohydrates production (Constable and Rawson, 1982). But inter-bolls competition equally persist for assimilates just like normal conditions and large size bolls compete effectively over emerging fruiting bodies which may detach from plant.

Table 2. Shedding losses (%) in cotton caused by various insects damage

Name	Scientific Names	Square/buds shedding (%)	Boll shedding (%)	References
Pink boll worm	<i>Pectinophora gossypiella</i> L.	3.3-7.7	0.2-1.7	Dhawan <i>et al.</i> (1990a)
Mirid bugs	<i>Creontiades biseratense</i> L.	11.27	4.81	Shalini (2010)
Tarnished plant bug	<i>Lygus lineolaris</i> L.	45.1	42.3	Teague <i>et al.</i> (2001)
Spotted boll worms	<i>Earias</i> spp. L.	12.5-16.6	7.9-9.5	Dhawan <i>et al.</i> (1990)

The excessive moisture from over irrigation or in form rainfall deprives the roots from oxygen supply and therefore, plants shorten the growth seasons by dropping the fruiting forms. The lower oxygen supply in the soil causes stomatal closure which reduces the photosynthesis and evaporative cooling and all this lead to increased fruit shedding. Therefore, it is strongly recommended that cotton growers must maintain the optimum moisture from commencement of squaring to peak flowering stage.

NATURAL COMPENSATION FOR SHEDDING

There is strong competition for assimilates between vegetative and reproductive structures over the growth season and hence, the preference to diversion of assimilates to various plant parts determines the survival of specific plant parts. By virtue of its fruiting pattern, the cotton plant compensates the loss associated with shedding by producing new fruiting forms next to that on fruiting branch. Either the environmental or biological factor that disturbs assimilates flow from source to sink or physically damage the flowers structure would promote the shedding.

Sometime, the yield is not necessarily reduced by shedding mainly because of compensation capacity of cotton from same or different branches. The time of season, growth stages and stresses determines the compensation level and it is much likely to occur early in season. The loss of few bolls (up to 30%) is acceptable because it can be compensated from newly one (Gutierrez et al., 1981; Pitman, 2000). Whereas, the compensation level for square ranged from 19-30% (Mi et al., 1998). The compensation may even be higher if temperature favors flowering and boll growth. By the compensation, the cotton has ability to produce even more bolls by increasing the length of sympodial branches in reduced plant population. It is explained by a mechanism referred as over-compensation. The compensation mechanism in response to early shedding is more prominent in non-BT varieties as compared to BT varieties. Therefore, early fruit retention in BT varieties is critical to achieve higher lint yield, while non-BT varieties can compensate later on. The said phenomenon is uncommon and occurs only if vegetative growth is poor and yield expectation is also low. The resulted better vegetative growth translates more production later in season. The fruit loss from shedding process alters the fruiting bearing pattern of cotton and its bolls were confined to outer portion at lower end and it concentrate fruiting in main stem proximity at the top portion.

The concept of active boll load also explains well the phenomenon of fruit shedding. For instance, cotton

cultivar H-6 retained maximum bolls up to 33 which gradually decreased with advancement in fruiting achieving no retention around 62 bolls per plant (Rabadia et al., 2006). It may be consequent of reduced food supply to individual boll like findings of Jackson and Gerik (1990) where boll carrying capacity was positively related to gains in leaf area. The increase in photosynthesis rate up to 15 % would result 50 % more bolls (Landivar et al., 1983). The abscission of fruiting forms favors the retention of next one by supplying additional assimilates from subtending leaves associated with abscised boll. The presence of boll at first position is sufficient to reduce the chances of retention of adjacent fruiting structures by limiting movement of assimilates. Even the newly emerging squares faces the competition among them and it has been noticed that survival rate of 2nd position boll on stalk is increased by 25-30% with shedding of boll at first position.

Depending on the time of shedding, it favors the portioning of plant resources to vegetative parts and there are significant chances that field gone vegetative in case of early season shedding. It may have following effects 1). It enhances the fruiting capacity later in season and to extend the growth period to unfavorable conditions and delay the sowing of next crop. 2). The above pattern of growth shades the bolls located at lower canopy and hence, boll retention at lower branches is reduced. 3). The application efficiency of pesticides and micronutrient is low because of low penetration in dense crop canopies. Such responses were more common with manual removal of four early squares per plant rather two square treatment. The crop management practices should be aimed to enhance the compensation mechanism to get reasonable yield after crop is relieved from stressful conditions. These include judicious use of growth regulator, irrigation and fertilizers. The shedding of early fruiting structures in late sown cotton is very harmful as recovery time shortened.

MANAGEMENT TOOLS

In the previous section of this article, we discussed the external and internal causes of shedding and looked at financial losses of this phenomenon. It was concluded that some environmental and biotic stresses induce the shedding other than natural and such type of shedding can be controlled to some extent by taken measures discussed below. The identification of cause is the most essential for the success of these management strategies.

The hormonal regulated shedding rate can be slow down by the application of their inhibitors. For instance, ABA stimulated abscission of fruiting

structures can be controlled with NAA (naphthalene acetic acid) which counteracted the ABA promotive effects. It was supported by the results of study conducted by Patel (1993) where application of triacontanol @ 2.5 ppm and naphthalene acetic acid (NAA) @ 10 ppm reduced shedding of fruiting forms by 22.5 and 18 %, respectively. Similarly, the role of 2,3,5-triiodobenzoic acid (TIBA) had been investigated for improving retention of flowers and buds in soybean. It had also been tested to be candidate of retention in cotton. It was sprayed @ 5 to 62.5 g/ha from first blossom to period of five weeks at one week interval. The lower doses were compensated by frequent and multiple application and significant increase in seed cotton yield from 8 to 16% was achieved. It had also been postulated that TIBA acts as inhibitor of auxin transport for endogenous production of ethylene (Freitag and Coleman, 1973). In the same way, Silver Thiosulphate ($\text{Ag}(\text{S}_2\text{O}_3)_2$) have potential to reduce shedding loss and its application @ 5-10 Mm during peak flowering increases 20-30% seed cotton yield (Prakash et al., 2007). Silver ion (Ag^+) in form of silver nitrate (AgNO_3) or as silverthiosulfate, 1-methylcyclopropene (MCP) and *trans*-cyclooctene are antagonistic to ethylene action, whereas, aminoethoxy-vinylglycine (AVG), amino-oxy-acetic acid (AOA) are well known inhibitor of ethylene synthesis.

The potential of plant growth regulators can also be used for reducing shedding losses by keeping vegetative and reproductive development in harmony. Mepiquat chloride (1,1 dimethyl piperidinium) is readily absorbed in foliage and redistributed in plants where it suppresses the synthesis of gibberellic acid leading to reduced cell division and enlargement (Srivastava, 2002). Therefore, its application to cotton may overcome the vegetative tendencies and improve retention on lower fruiting branches. The biweekly applications of Mepiquat chloride (MC) @ 24.5 g ha^{-1} at early bloom stage reduced the excessive vegetative growth and improve the fruiting on lower sympodia (Cook and Kennedy, 2000). However higher application rate of mepiquat chloride during peak flowering must be avoided to permit production of fruiting sites for yield compensation (Yeates et al., 2002). Its application in moisture stressed field or areas not receiving post application rains, must be avoided to put off onset of additional stress which would cost a significant yield loss.

Girdling is another promising technique to retain fruiting structures and its application during flourishing stage reduce shedding losses up to 15.8% over control (Qiang et al., 2014). However, this technology is labor intensive and its adaptation at large scale is much difficult.

Under stressful and heavy pest infestation, the contribution of internal plant factors to shedding is much less important. It can be minimized by maintaining soil nutrition by balance fertilization, avoiding stresses, water logging and rank growth, spray of nutrient solution and PGR, adjusting the sowing so that peak flowering must not coincide with high temperature, drought and rainy period and adopting plant protection measures in crucial period. In Indo-Pak region, the seasonal sown crop produces flowers in the month of September contribute to 50% yield and crop growth should be critically monitored for shedding rates.

CONCLUSION

The shedding in plants is natural ability to throw off fruiting structures/leaves in view point of assimilate supply and demand balance. The cotton plant adjusts boll load by dropping 50% of premature boll load naturally and this may increase with the provision of stressful conditions. The rate of shedding is accelerated by the plant internal processes that provoked in response to stresses imposed by environmental conditions such as drought, water logging and high temperature. For such factors to be successful mediator of shedding of fruiting structures, it is bolls age along with the probability of shedding is negatively affected. Therefore, the flowers and immature bolls are more likely to shed than mature ones. The cotton plant has ability to compensate the shedding loss by producing more fruiting sites and retaining the bolls later in growth season if environmental conditions support the growth. The yield loss by shedding can be prevented by keeping away the biotic and abiotic stresses and application of plant growth hormone well in time.

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