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RESEARCH ARTICLE

The Photoperiodic Floral Transition in Cotton (*Gossypium hirsutum*)

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ABSTRACT

The wild races of *Gossypium hirsutum* is a tetraploid perennial plant and follows short day photoperiodism for flowerings. But upland cotton, which is cultivated in most parts of world, insensitive to photoperiodism. The flowering or reproductive stage in *Gossypium hirsutum's* life cycle is important for cotton fiber formation. However, upland cotton is insensitive to the process of photoperiodism but its critical to understand the floral transition process, structure of cotton flower at microscopic level and effect of environmental factors on its flowerings so that it may help scientists in several other processes like speed breeding or to develop good varieties of cotton because fruiting is next stage of flowerings in cotton plant. Many circadian clock genes in cotton plant express according to sunlight duration, temperature, age, and hormonal changes. Cotton flowers at a certain age. Several genes, such as circadian clock genes in cotton leaves, control flowering circumstances such sunshine length, temperature, and more. Phloem transports reproductive signals from cotton leaves to shoot apex. Floral identity genes activate floral identity organ genes that generate cotton flower parts. The photoperiodism in *Arabidopsis thialiana*, which is considered as model plant also help to understand the photoperiodism in cotton at microscopic and genetic level.

Key words: Photoperiodism, Flowerings in cotton, Floral transition, Microscopic structure of cotton flower, Genetic studies

INTRODUCTION

Most of the studies on Gossypium are focused on tetraploidy in cotton species like *Gossypium hirsutum* and *Gossypium barbadense* (i.e 2n = 52) or on diploid Gossypium species like *Gossypium raimondii* and *Gossypium arboreum* (i.e 2n = 26) (Zafar et al., 2024). *Gossypium hirsutum* is a tetraploid semi-wild race. These semi-wild races are sensitive to short-day photoperiod while cultivated upland cotton is insensitive to photoperiod (Kushanov et al., 2017). The sensation to photoperiod in wild and semi-wild races of cotton has great importance especially when vegetative phase of cotton transits into reproductive phase (or simply floral transition) (Grover et al., 2020). The *Gossypium hirsutum* cultivated more than in 80 countries (Khan et al., 2020). So, this review is mainly discussing the floral transition of semi wild *G. hirsutum* and upland cultivated *G. hirsutum*.

Many circadian clock genes show their expression according to sunlight duration, temperature, age and many hormonal changes in cotton plant (Johansson and Staiger 2015). The cotton shows flowering when reached to a specific age. Many genes take part in this transition like circadian clock genes which usually present in the leaves of the cotton determines the conditions for flowerings such as sunlight duration, temperature etc. (Li et al., 2022). The reproductive signals from leaves of the cotton moves towards shoot apex through phloem. The flower identity genes then activate the flower identity organ genes that make different parts of cotton flower (De Moura et al., 2020).

Gossypium hirsutum have different developmental stages during their life cycle. First stage is immature vegetative stage. In this stage, the whole plant body of cotton plant present in its vegetative form. No floral reproductive signals are produced in cotton plant

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during this stage. It starts from seedling and continues with time, until the plant is matured (Chen et al., 2016). Adult vegetative or mature vegetative stage is the second stage in this transition where reproductive signals are started to arise from leaves of the cotton. These signals then moved towards shoot apex where they started to form the reproductive structure of cotton plant (I.e. cotton flower) (Tharp 1960). These reproductive signals are generated by photoperiodic pathway in cotton plant which activates floral meristem identity genes (Li et al., 2020). The photoperiodic flowering mechanism is mainly divided into three parts I.e. light input (senses by photoreceptor), circadian clock (floral responses/changes in plant according to environment), and output (flowering in plants) (Grover et al., 2020).

Photoperiodism in Cotton (Light Input)

The photoperiodism is the response shown by plants against light availability and day-night duration. The photoperiodism is mainly controls the flowerings in plants, fruit and seed formation and also seed dormancy and germination (Lumsden 2002). The process of photoperiodism is regulated by many photoreceptor like phytochrome, cryptochrome and phtotropin in cotton plant (Möglich et al., 2010). The semi-wild races like *Gossypium hirsutum, Gossypium barbadense, Gossypium raimondii, Gossypium arboreum* are short days sensitive and show short-day photoperiodism. While the cultivated upland cotton (like *G.hirsutum*) are insensitive to photoperiodism or day neutral plants (Gowda et al., 2023).

Phytochromes

The phytochromes are red and far-red photoreceptor that regulates numerous growth and developmental process in cotton (*G.hirsutum*) like photoperiodic flowering, fiber development and plant architecture as well by releasing chemicals that triggers these processes (Wells 2011). Two different forms of phytochrome exist in cotton plant. One is active form (Pfr) while the other is inactive form (Pr). Both these forms are inter-convertible according to the wavelength of light (Quail 2010). The Pr (cyan blue in color) form of phytochrome is inactive form but after sensing and absorbing red light (620-700 nm) it converts into Pfr (cyan-green color), an active form of phytochrome. In the same way, the Pfr after absorbing far-red light (710-850 nm) changed into inactive form (i.e. Pr) (Casal et al., 1998). The process of this conversion according to the wavelength of light is called photo reversibility (Burgie et al., 2020).

The phytochrome consists of two structures. One is chromophore (phytochromobilin) that absorbs light while the other is poly peptide part (protein). Both these structures are linked together covalently and form the inactive form of the phytochrome. The active form is the dimer of two sub units of inactive form of phytochrome (Li and Hiltbrunner 2021). The active phytochrome has large molecule of apoprotein that binds with phycobilin chromophores. The apoprotein is encoded by four gene families phytochrome-A (PHY-A), phytochrome-B (PHY-B), phytochrome-C (PHY-C), and phytochrome-E (PHY-E) in cotton (Abdurakhmonov et al., 2010).

The GhPHYA is light unstable and so work in dark or night (Miao 2016) while GhPHYB is the most abundant as it work in both day and night (Rao et al., 2013). The GhPHYC and GhPHYE are also light stable (Abdurakhmonov et al., 2010). For the expression of GhPHYA, it has to be moved inside the nucleus. This movement is facilitated by FHY-1 protein. While in the case of PHYB protein, it can move directly inside the nucleus as it has Nucleus Localizing Signal (NLS) which guides PHYB to move inside the nucleus so that it can express its function (Li et al., 2022). A complete structure of phytochrome has two regions, one is photo sensory region that senses the light while the other is response regulator region that produces response in the plant body according to the message from sensory region (Ulijasz et al., 2011).

The fiber length increases with the increase in ratio of far-red to red light acceptance (Lei et al., 2024). Miao (2016) reported that silencing of PHYA1 gene by RNA interference generated with RNAi cotton lines have phenotypic characteristics like early flowering, improved fiber quality, vigorous roots and vegetative growth, high tolerance against some abiotic stress without any adverse effect on yield and fiber development.

Cryptochrome

Cryptochromes are the photoreceptor that sense blue-light from environment. Like phytochrome, it also has photo sensory region that sense the blue light and a response region that is made up of proteins and produces responses in the cell according to the wavelength and intensity of light (Schneps et al., 2024). The photo sensory region of cryptochrome is composed of mainly two sub units I.e. flavin and pterin (MTHF). The responsory region of cryptochrome produces responses in plant like inhibition of stem elongation, leaf expansion etc. after sensing the blue light by photo sensory region (Wang and Lin 2020).

GhCRY1 and GhCRY2 are the two types of cryptochrome genes that is present in the nucleus of the cotton plant. GhCRY1 regulates stem elongation. It inhibits stem elongation once it senses the blue light from environment. GhCRY1 expression is enhanced by the intensity and duration of blue light from sun. The cryptochrome also regulates the flowering in cotton plant. The GhCRY2 binds with CIB1 and forms GhCRY1/CIB1 complex. The CRY2 and CIB1 complex binds at the promoter side of FT gene and started to transcribe it and make mRNA from FT-gene (Omelina et al., 2022). The mRNA of FT is translated and make proteins. These proteins move towards shoot apex through phloem where they act as flowering signals from leaves of the cotton plant.

Phototropins

Phototropins are membrane associated molecules that senses the blue light from environment. They are flavo-proteins in nature. Flavin has FMN (Flavin Mono-Nucleotide) that sense the blue light from environment (Hart et al., 2021). The protein region is the response region that is encode by two different genes in cotton. One is GhPHOT1 and other is GhPHOT2 (Labuz et al., 2022). The GhPHOT1 show its expression under low intensity blue light. While GhPHOT2 express itself when there is high intensity of blue light is present. The phototropins involves in the responses like chlorophyll movement in the leaf, leaf expansion and stomatal opening etc. in cotton plant. Chlorophyll movement necessary for better growth (Sztatelman et al., 2016). As chlorophyll can be damage by high intensity sunlight so it show avoidance response with respect to high intensity light rays (Ouzounis et al., 2015). This kind of chloroplast response is regulated by phototropins. While when plant is receiving low intensity of blue light then chloroplast show accumulation response which also regulated by phototropins (Łabuz et al., 2015).

A very complex interconnected system is seen in the floral transition in which different photoreceptor sense different wavelengths of light and generate different responses or changes in plant's body according to external light conditions (Sreekantan et al., 2010). These responses activates and regulates different clock genes (Jarillo and Piñeiro 2011). The term "clock genes" is specifically used for that genes because they show their specific phenotypic expression like floral transition or flowerings in plants only in specific day-night duration or light signals (Kinmonth-Schultz et al., 2013). The expression of these genes regulates activity of flower meristem identity genes in cotton plant (Naveed et al., 2023). The flower meristem identity genes make changes at shoot apex of the cotton plant and regulate the expression of flower organ identity genes (Feng et al., 2021) which then form a complex inter-connected system and produce cotton flowers at the shoot of the cotton plant (Naveed et al., 2023).

Circadian Clock Regulation (CO-FT-FD Module)

The CONSTANTS-FLOWERING LOCUS-T (CO-FT) module is the central integral of photoperiodic pathway for flowerings in many plants (Pin et al., 2012) and is highly conserved in short-day cotton plants like wild cotton because they are highly sensitive to photoperiodism. High CO level in cotton regulates expression phenotypically of FLOWERING LOCUS-T (FT) genes. Expression of FT genes are necessary for flowerings in cotton plants. The CO-FT module is controlled by light signals and circadian clock genes (Nazir et al., 2024). Different photoreceptor participates in sensing the external light and generates changes in the plant body according to environmental conditions in cotton plant. These changes express different clock genes of the plant body. The expression of these clock genes regulate vegetative phase to reproductive phase transition in different plants including *Gossypium hirsutum* by generating floral signal through different pathways (Li et al., 2022).

Arabidopsis Flowering CO-FT-FD Module

In *Arabidopsis thaliana*, which is considered a model plant because it mostly flowers in spring season by sensing the day-night duration. The circadian clock is tissue specific and it varies with different plants. Like in the case of *Arabidopsis thaliana*, the vascular circadian genes mainly responsible for flowering photoperiodism (Shim et al., 2017). The messenger RNA of CO, in phloem companion cells of leave is regulated at transcription level through many circadian clock-regulatory components like F-box (Flavin Binding Kelch Repeat), GI (Gigantea) and CDFs (Cycling Doc Facters). The down regulation of CDFs promotes CO in plants (Imaizumi et al., 2005). During daytime, the CDFs started to induced in the plant by LHY and CCA1. while in afternoon, the concentration of CDFs is regulated by PRR5, PRR7, PRR9 as they decreased the concentration of CDFs at that time. The CDFs circadian regulation is controlled by FKF1, forms complex with GI (Fowler et al., 1999) (i.e. FKF1 + GI complex) (Sawa et al., 2007). This complex is well synchronized at the end of the day

Table 1: Functions of different photoreceptor in *Gossypium hirsutum* reported by different scientists (Li et al., (2022); Grover et al., (2020); Abdurakhmonov et al., (2010); (Miao 2016); Rao et al., (2013); Lei et al., (2024); Miao (2016).

Photoreceptor genes	Functions
GhPHYA1	Light unstable gene. Silencing of GhPHYA1 can promote early flowering and improve cotton fiber quality
GhPHYA2	Light stable and very abundant in cotton plant. Involves in the regulation of flowering and improve the yields of cotton
GhPHYB	Light stable photoreceptor
GhPHYC	Light stable photoreceptor
GhPHYE	Light stable photoreceptor
GhCRY1	Regulates stem elongation Stabilize the CO-protein complex at the end of the long day
GhCRY2	Binds with CIB, helps in the transcription of GhFT genes that promotes flowering in cotton plant Stabilize the CO-protein complex at the end of the long day
GhPHOT1	Show accumulation response of chloroplast under low intensity blue-light which is essential for the absorption of more light by chloroplasts of the cotton plant's leaves.
GhPHOT2	Show avoidance response of chloroplast under high intensity blue-light which is essential for the protection of chloroplast from these high intensity rays.

in blue light. The resulted protein of this complex (FKF1 and GI) make more deviation in the concentration of protein of CDF at the end of the day. The depression or deviation in CDF protein regulates the concentration of CO-protein. More the depression in CDF protein concentration, more will the CO-protein concentration these plants. During short days the FKF1 and GI complex was not as much effective because FKF1 is mostly expressed in dark and the balanced concentration needed for FKF1 and GI complex is not achieved (Imaizumi et al., 2005). As CO-protein concentration is proportional to FT, so more the CO-protein is produced in the plant, more FT-protein will be produced. The FT-proteins move towards shoot apical meristem, it acts as floral signals from the photoreceptor of leaves and this leads to the flowerings in *Arabidopsis thaliana* (Turck et al., 2008).

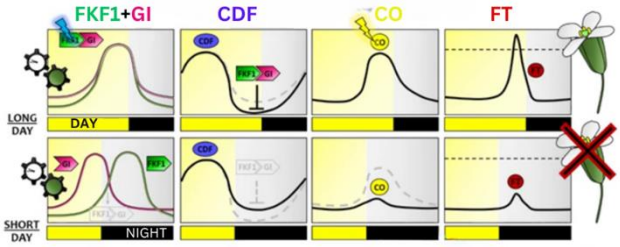

Fig. 1: Sawa et al., (2007); Fowler et al., (1999) reported circadian clock regulatory pathways of *Arabidopsis thaliana* for floral transition. It shows up and down concentrations of different regulatory components like FKF1, GI, CDF in both short and long days and also their effect on CO-FT concentration that produces flowering signals in *Arabidopsis thaliana*. The FKF1 interacted with GI and form a FKF1/GI complex. The concentration of both FKF1 and GI matters for the flowering in Arabidopsis. During summer, the concentration of FKF1 and GI is very balanced and this balance is essential for the repression of CDFs factors that negatively regulate the CO-transcription in Arabidopsis. During winter or short days, the balanced between FKF1 and GI was not achieved and so the deviation in the concentration of CDFs was not as much to triggers the FT through CO-protein. This shows that flowering in *Arabidopsis thaliana* can be attained in long days only.

The CO-protein is also regulated with the photoperiodism in *Arabidopsis thaliana*. Like during day time, red light receptors phytochrome B involves in decay of CO-protein (Rao et al., 2011). The E3 ubiquitin ligase helps the PHYB in this degradation. While at evening, the blue light blocks proteolysis of CO-protein through CONSTITUTIVE PHOTOMORPHOGENESI (COPI). Blue light receptor cryptochromes (Liu et al., 2008) and far-red light receptor PHYA stabilize the CO-protein at sunset. This CO-protein then regulates expression of FT which produce floral signals (Bouche et al., 2016).

Cotton Flowering COL1-FT-FD Module

The CONSTNAT LIKE-1 (GhCOL-1) is the activator of FLOWERING LOCUS-T (GhFT) in cotton plant (*G. hirsutum*). In the morning time, the expression rate of both GhCOL-1 and GhFT is increasing. The regulation expression by circadian clock of both GhCOL-1 and GhFT have involvement in flowerings (Guo et al., 2015). High level of GhFT encodes the member of phosphatidylethanolamine amine binding protein. Cai et al., (2017) reported that GhCOL1-A and GhCOL1-D have important role in cotton flowerings. While some other COL1 genes like GhCOL3-A, GhCOL3-D, GhCOL7-A, GhCOL7-D partially reversed the delay in cotton flowerings.

In cotton (*G. hirsutum*), GhLUX1 and GhELF3 are also two circadian regulators. Silencing both genes increased the expression of COL1 (CONSTANT LIKE-1) and FT (FLOWERING LOCUS-T) which results the early flowering in cotton. It has also been revealed from studies that GENERAL REGULATORY FACTORS (GRFs) involved in the flowerings of cotton (*G. hirsutum*). GhGRFs interacted with GhFT in nucleus and cytoplasm. They also show interaction with GhFD in nucleus of cotton plant cell (Sang et al., 2021). The GRFs gene family regulates the flowerings of cotton (*G. hirsutum*) by inhibiting and promoting it. Such as genes like GRF3, GRF6, GRF9 and GRF15 when interacted with GhFT and GhFD, the resulted FACs inhibits the flowerings. While the gene GhGRF14 interacted with GhFT and GhFD to form Florigen Activation Complex (FAC), promotes flowerings in cotton plants and regulates the floral meristem identity genes like GhAP1, GhSOC1.

FT-genes involves in the encoding member of phosphatidyl-ethanolamine-binding-protein (PEBP) gene, produces mobile signals in the cotton plant. Zhang et al., (2016) reported that PEBP genes belonged to four sub-clades i.e. FT, MFT, TFL1 and PEBP. The FT/TFL1 like genes were basically participate in flowering time regulation while the MFT-like genes mainly involve in seed development. GhFT is a floral activator gene while GhTFL1 is floral repressor (Prewitt et al., 2018). In the vegetation phase, the transcripts of TFL1 accumulated in inner cells of mature meristem. It acts as a mobile signal that travels from the inner shoot meristem to outer shoot meristem, synchronizes with shoot meristem identity genes and make the architecture of the plant by interacting with FLOWERING LOCUS-D (FD) genes. Tissue specific expression studies related to GhPEBP in *G. hirsutum* showed that GhPEBP1 and GhFT transcripts levels are high in bud and flowers as compared to other vegetative organs of cotton plant. Transcript level of GhPEBP2 was high in leaves, shoot apical, buds and flowers. However, GhPEBP2 had no consistent effect on flowerings (Wang et al., 2019).

The GhFT expression was induced in short day cotton plant while GhPEBP2 was introduced in long day. Also, the GhPEBP2 was not interacted with FLOWERING LOCUS-D (GhFD-like) bZIP transcription factors (that promotes flowerings). The transcript of GhFT1 shows diurnal oscillation expression in long day and short days conditions which shows that the

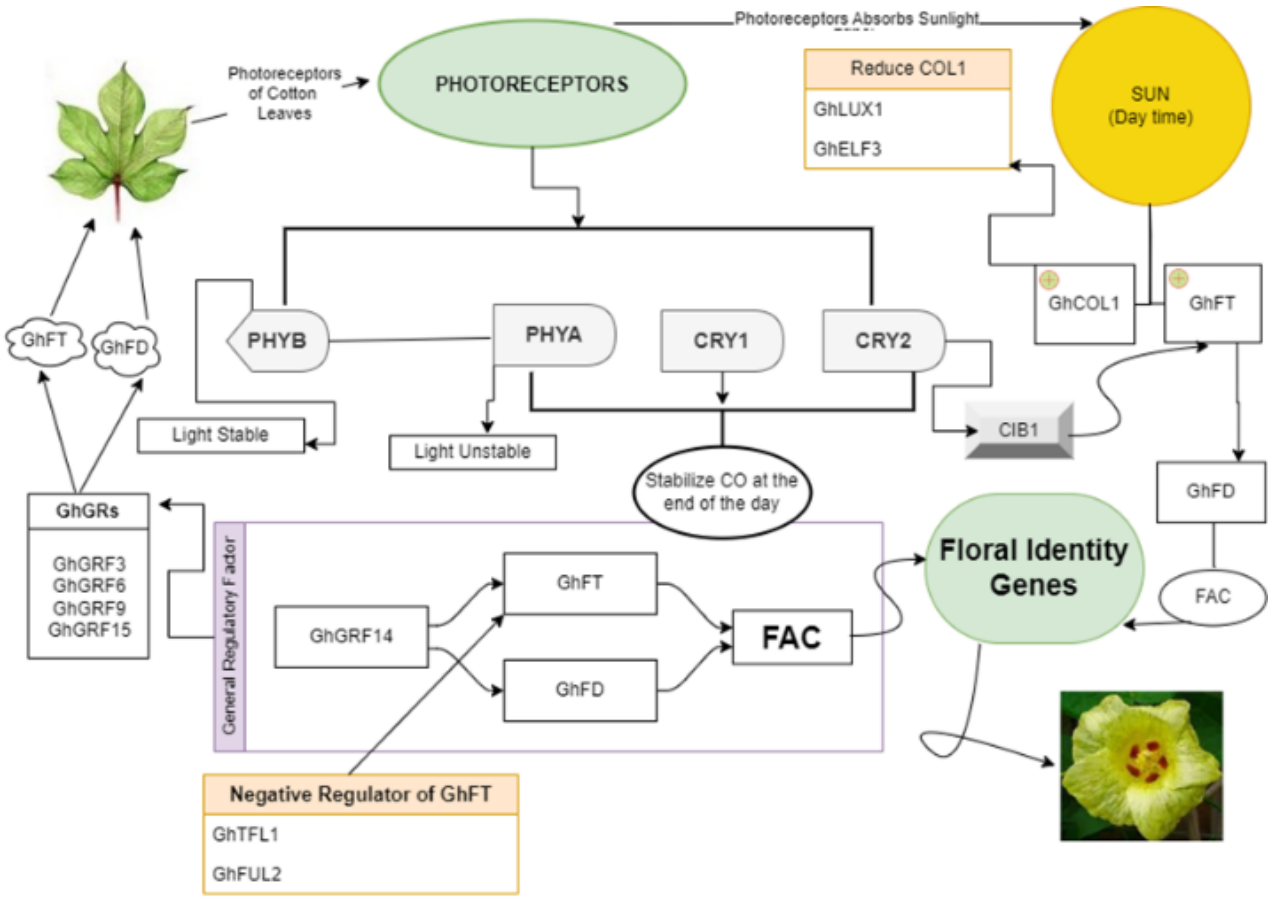

Fig. 2: Involvement of different genes and transcription factors in the flowerings of cotton. Sunlight is received by the photoreceptor of cotton leaves. These photoreceptor (PHYA, PHYB, CRY1, CRY2) then generate responses according to the wavelength of light. The PHYA is the light unstable photoreceptor means show its expression at night while PHYB, CRY1 and CRY2 can show their expression in the presence of light but CRY1 and CRY2 are blue light photoreceptor. The PHYA, CRY1 and CRY2 at sunsets, which stabilize the CO-protein concentration that helps in the transcription of GhFT gene. The CRY2 can interacts with CIB1 factors that can also help in the transcription of GhFT gene. The GhFT gene is also transcribed by GhGRF14 that can also interacted with GhFD and promote flowering in the cotton plant. Some negative floral regulators are also show in this figure such as GhTFL1, GhFUL2 negatively regulate GhFT. While GhLUX1, GhELF3 repress the concentration of CO-protein in cotton plant. The GhGRF3, GhGRF6, GhGRF9, GhGRF15 promote vegetative structure (leaves) in the cotton plant The whole information in this figure is reported by many scientists Guo et al., (2015); Cai et al., (2017); Hao et al., (2021); Sang et al., (2021).

expression of this gene under circadian clock. Guo et al., (2015) reported that GhFT1 were highly expressed in stamen, sepal, petal, pistil and also in the fiber of cotton. It also shows its presence in ovule, root, leaf and stem. Research proved that silencing of GhFUL2 (FRUITFUL 2) in cotton can increase the expression of GhFT and GhMADS42, that promotes flowerings in cotton. So GhFUL2 is negative regulator of flowering (Zhang et al., 2021). GhFUL2 interacts with GhSEP and GhSVP to regulated the flowering genes like GhLFY, GhFT, GhMADS42 etc.

The GhFT proteins interacted with FD-transcription factors at the shoot apex and promote flowering in that region. The FT genes transcribed and produces messenger mRNAs (mRNAs). These mRNAs then translated and form FT-proteins. These proteins travel towards shoot apical meristem (SAM) through phloem. The FT proteins activate and synchronize with flowering locus-D (i.e. bZIP transcription factor) and form a FT/FD complex, which regulates SUPRESSOR OF OVEREXPRESSION OF CONSTANT1 (SOC1) and floral meristem identity genes I.e. LEAFY genes, APITALA genes, CAULIFLOWER genes, AGAMOUS genes of cotton plant.

The Transition of Cotton Flowering Buds into Flower (Output)

As flowers arise on reproductive branches that is well differentiated from vegetative branches of cotton plant, however the floral signals and floral transition occurs by these vegetative branches. The cotton flowering buds are originate only on the reproductive branches of cotton plant (Chen et al., 2024). Different genes participates in the regulation and activation of FT/FD complex in the cotton plants which is the major component that reprogram SAM, form floral primordia instead of leaf primordia on the branches of cotton (McGarry et al., 2012). Axillary bud primordia is the key decider that form leaf primordia as well as flower primordia according to environment, day-night period, plant's age etc. (Shi et al., 2020). Four whorls of a flowering bud appear on the axillary bud of cotton

Table 2: The functions of different genes and transcription factors that play their role in cotton flowering reported by different scientists.

Genes/Factors	Functions
GhCOL1-A	Induce flowering in cotton, reversed late flowering phenotype
GhCOL1-D	Induce flowering in cotton, reversed late flowering phenotype
GhCOL3-A	Partially rescued/reversed late flowering phenotype
GhCOL3-D	Partially rescued/reversed late flowering phenotype
GhCOL7-A	Partially rescued/reversed late flowering phenotype
GhCOL7-D	Partially rescued/reversed late flowering phenotype
GhGI (GIGANTIA)	Circadian clock-regulatory component
GhFKF1	Circadian clock-regulatory component
CYCLING DOC FACTORS	Circadian clock-regulatory component
GhLUX1	Circadian clock regulatory component, silencing of this induce early flowering in cotton
GhELF3	Circadian clock regulatory component, silencing of this induce early flowering in cotton
GhFT1	Its expression level was high in stamen, sepal, petal, pistil and fiber of cotton. It also expresses in ovule, root, leaf and stem.
GhPEBP1	Transcripts level of GhPEBP1 was high in bud and flower as compared to other vegetative structures of cotton plant
GhPEBP2	Transcript level of GhPEBP2 was high in leaves, shoot, apical buds and flowers
GhGRF14	It interacted with GhFT and GhFD, and the resulted FAC (florigen activation complex) leads to the flowerings in cotton
GhFUL2	Negative regulator of flowerings in cotton
GhGRF3	Interact with GhFT and GhFD, the resulted compound inhibits flowerings
GhGRF6	Interact with GhFT and GhFD, the resulted compound inhibits flowerings
GhGRF9	Interact with GhFT and GhFD, the resulted compound inhibits flowerings
GhGRF15	Interact with GhFT and GhFD, the resulted compound inhibits flowerings

when plant is going to form flower primordia on it. The inner most whorl makes female reproductive part (i.e. carpel). The next or upper whorl makes male reproductive parts (i.e. stamens). The whorl just inside to the outermost layer form's petals of the flowers while outer most whorl form sepal of flower. This will be the initial physical structure of cotton flowering bud that can be seen. The floral morphology of *G.hirsutum* comprise pedicellate, sympetalous with three green bracts, a calyx whorl, 5 petals, 4-5 locule capsule in which 6-9 ovule develops (Mauney 2015).

De Moura et al., (2020) reported the floral primordia differentiation is driven by axillary bud primordia. Firstly, floral meristem dome is surrounded by sepal primordia forming a spheroid structure around floral meristem. Then this sepal primordia covered the petal primordia meristem and staminal column differentiated. Early stages of stamen primordia can be observed which is fused at base and surrounded by both sepal and petal premedia. At the second stage of cotton flowering bud, the large bracts of sepals and petals can be observed. Sepals covers the stamens on which anthers are compactly arranged. The presence of anthers and ovule primordia delimits this stage of flowering bud from the initial one. At the third stage of cotton flowering bud, the outer floral organs, sepals and petals grows in size and petal covers the whole androecium and gynoecium. The male reproductive parts, anthers and female reproductive part, ovule grow inside these outer floral organs.

Anther Developmental Stages in Cotton (*G. hirsutum*) Plant

De Moura et al., (2020), reported the anther development is carried with microsporogenesis and micro gametogenesis. At the initial stage stamen primordia is formed. Once the filaments and staminal column is formed, the developmental process of anther is started. The bilocular anthers observed after its development. At this stage, archesporial cells and parietal layers are observed. Then the differentiation started between sponogenous cells, filaments and connective tissues on stamen. All the cell layers of anther wall such as epidermis, endothecium, middle layer and tapetum, are well distinguished. The sporogenous cells are then differentiated into microspore mother cells (PMC). Also, high deposition of cellulose is observed in the flowering buds of cotton in this stage. With the end of deposition of cellulose, the tapetum cells started to increase their size. Then cotton anthers enter into the next stage of its development. The microspores from microspore mother cells are started to release from the tetrads. With the release of the microspores, the nucleus started to move at the periphery due to large size vacuole. The tapetum started to degenerates and formation of fibrillar material around the microspore walls is observed. Microspores at this stage of another development, exhibit exine with echinate ornamentation. Microspores continues to display exine with echinate ornamentation until only epidermis and endothecium cell layers remains in the anthers of the cotton (G. hirsutum). lignification of endothecium is clearly visible at this stage. The stigmatic papillae are well developed and the final sporogenesis morphology of the anther of cotton flower is evident. In the last, the mature pollen grains exhibit highly echinate ornamentation.

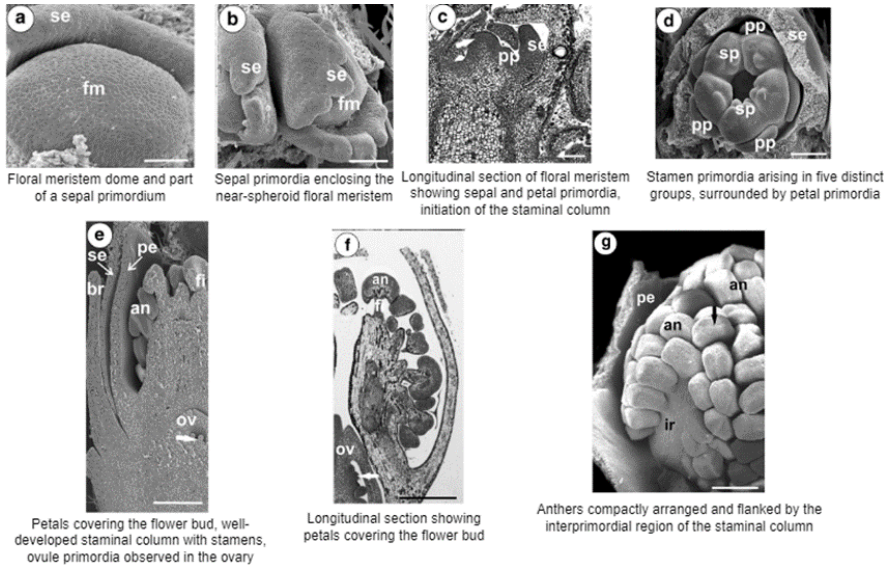

Fig. 3: De Moura et al., (2020) reported different stages of flower bud development at microscopic level. Image a in this figure show the floral meristem (fm) and sepal primordium (se). Image b in the figure show sepal primordia enclosing the near-spheroid floral meristem. Image c in the figure show the sepal and petal primordia (pp). Image d in the figure shows the arising of stamen primordia (sp) that is surrounded by petal primordia. Image e in the figure show the view of floral bud in which bracts (br), anther (an), ovule primordia (ov), petal and sepal primordia can be seen. The image f of the figure shows the longitudinal section of floral bud. The image g of the figure shows the arrangement of anthers.

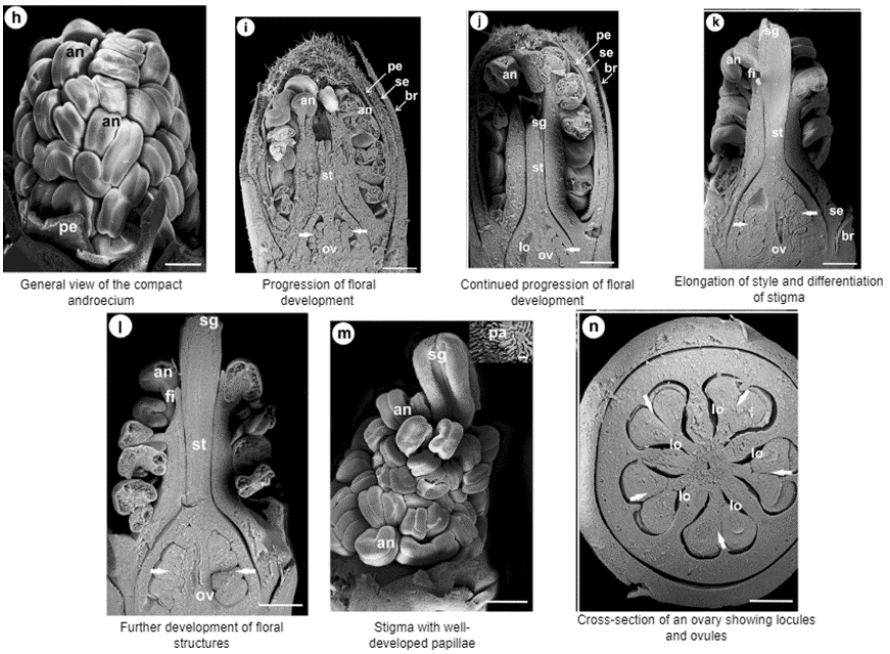

Fig. 4: De Moura et al., (2020) reported the developmental stages cotton floral bud at microscopic level. The image h of this figure shows a general view of compact androecium. The image I show a longitudinal view of progression of floral development. The image j shows progression of floral development at advanced stage. The image k shows elongation of style from the floral bud. The image l shows further developmental stages of flower of cotton. The image m shows the well development stigma on anther (male reproductive part) of the flower. The image n shows a cross section of ovary (female reproductive part) which show locules and ovules in the ovary.

Ovule Developmental Stages in Cotton (*G. hirsutum*) plant.

There are five fused carpels (locules) present in *G. hirsutum* ovaries. Two rows of ovule formed within each locule. Ovule development begins with the emergence of early ovules within the ovary locules where seminal rudiments emerge from the placental zone. This ovule development begins at the second stage flowering bud development. The process of ovule initiation starts from bottom and two different cell layers are formed. The outer layer form outer integument and the inner layer form inner integument with a central area. The archesporial cells with dense nucleus can be observed at this stage. This ovule primordia continue to develop, projections of outer and inner integuments by anticlinal and oblique divisions are observed at the end of this stage. These archesporial cells then form megaspore mother cells (mega sporocyst). Then both integuments and the nucellus start to develop. Later this, the integuments surround the nucellus such as the outer integument growing over the inner integument until the integument covers the whole nucellus. Then the functional megaspore which is located chlazal pole, indicate beginning of mega gametogenesis. This mature flowering bud of G. hirsutum shows anatropous ovule. The ovule continues to develop and micropylar region is established in mature ovules (De Moura et al., 2020).

Genes Involve in the Transition from Flowering Bud to Flower

GhRPD3

The GhRPD3 (Reduce Potassium Dependency 3), which is the category of HDACs (HISTONE DE-ACETYLASES) involved in cotton flower bud differentiation and also involved in the fiber initiation of cotton (Wei et al., 2021). HDACs are divided into three main categories I.e. RPD3 (Reduce Potassium Dependency 3), HDA1 (Histone De-Acetylase 1),

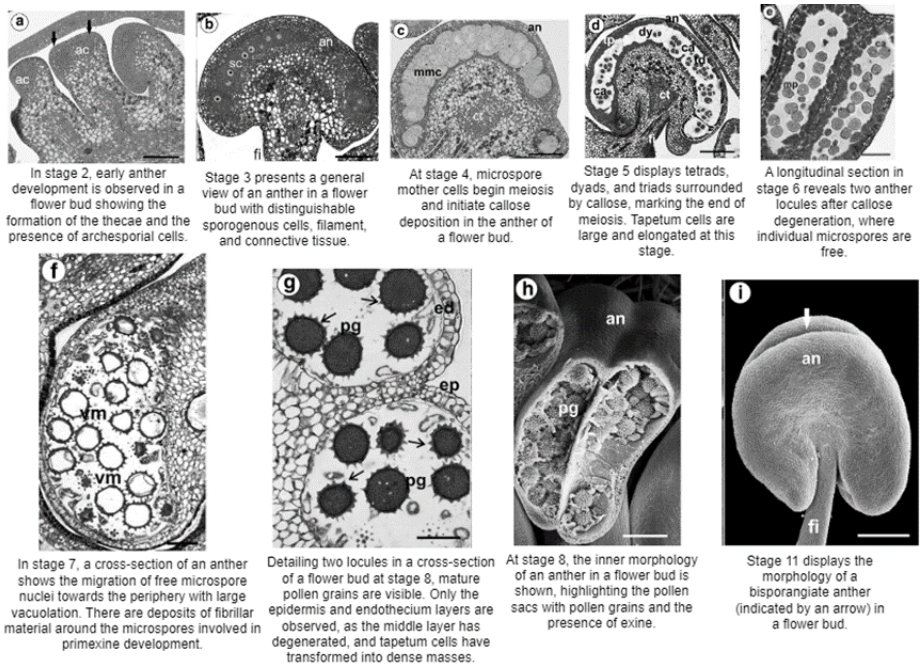

Fig. 5: De Moura et al., (2020) reported the developmental stages of anther in the cotton plant at microscopic level. The image a showing second stage of anther development, the early anther development is observed. Image b representing the third stage of anther development in which anther with distinguishable sporogenous cells, filaments and conductive tissues can be seen. The image c discussing the fourth stage of anther development at which microspore mother cell begins meiosis. The image d showing the fifth stage of anther development in which the tetrads, dyads and triads surrounded by callose. Tapetume cells enlarged and elongated at this stage. The image e representing the sixth stage of anther development by showing two anther locules. The image f showing the seventh stage in which a cross section of anther is shown. The microspore nuclei migrate towards periphery by large vacuole. The image g and h of this figure represents the eighth stage of anther development. While the image I showing the morphology of bisporangiate anther at stage eleven of the anther development.

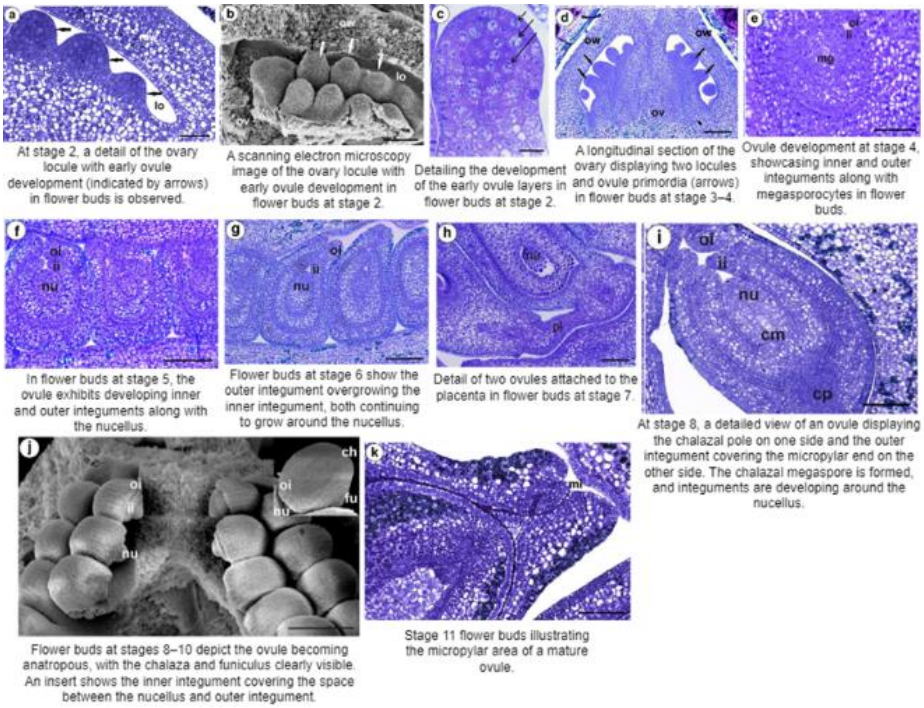

Fig. 6: De Moura et al., (2020) reported the developmental stages of ovule development in cotton floral bud. The image a, b, c of the figure showing the early ovule at second stage of its development. The image b represents the ovule at second stage by electron microscope. The image d explaining the third and fourth stage of ovule development. The image e showing fourth stage of ovule development in which inner and outer integuments can be seen. The image f representing the fifth stage of ovule development. The image g explaining the sixth stage of development in which outer-integument growing over the inner integument and cover the nucellus. The image h representing the seventh stage of ovule development. The image I showing the chlazal megaspore at stage eight. The image j represents the eight to ten stage of ovule development while the image k represents the stage eleven in which flower bud illustrates the micropylar area of mature ovule.

HDA2 (Histone De-Acetylase 2) and SIR2 (Silent Information Regulator) (Ma et al., 2013). Jia et al., (2023) reported that in *Arabidopsis thaliana* AtHDA19 was participate in various functions like seed development, circadian clock regulator and also in flowerings of *Arabidopsis thaliana*. It also involved in the regulation of gene expression related to jasmonic acid pathway and ethylene signaling pathway in the response of pathogens and wounds. This show the importance of RPD3 family in the developmental processes (Kumar et al., 2018), hormone regulation (Imran et al., 2019) and also in various stress conditions in plants (Bano et al., 2023). The GhRPD3 genes are widely expressed in both vegetative and reproductive parts of the cotton showing the importance of this gene (Zhang et al., 2020).

GhSOC1/LFY/AP1/SPL/AGL/FUL

The SOC1-like gene family of cotton plays as important role in flowering time as well as the floral organ development in cotton (*G.hirsutum*) plant (Ma and Yan 2022). The GhSOC1-1 shows its expression in normally short days and also under the conditions like high temperature. The over-expression of GhSOC1-1 also up regulate the expression of GhLFY in cotton plants which plays an important role in floral transition of cotton. The GhSOC1 interacted with GhAGL24 to regulates the expression of GhLFY directly (Lee et al., 2008). While GhSOC1-2 activates in long days. Another SOC1 family genes, GhSOC1-3 responds under cold conditions and also in long days (Ma and Yan 2022). Dow regulation of GhSOC1s-like genes result in the delay of flowerings in cotton (Naveed et al., 2023). The GhLFY present in the nucleus of plant cell and show its expression at shoot apex during floral bud differentiation (Jin et al., 2021). The CHIP assay results shows that the interaction between GhLFY and GhSOC1 may be similar to that of the interaction in Arabidopsis because GhSOC1 regulating the GhLFY in cotton and this same kind of regulation is present in Arabidopsis (Li et al., 2013). The chromatin immunoprecipitation assay of GhSOC1 reveals that it regulates GhMADS41 and GhMADS42 directly by binding to genes promoter. The expression of GhSOC1 and GhMADS42 were observed in leaves, flowers and shoot apical buds of the cotton which clearly highlight its involvement in floral transition and floral development. The GhMADS42 can also promote flowerings (Zhang et al., 2016). However, the GhSOC1 interact with other MADS-box genes like APITALA-1 and FRUITFULL-like proteins in cotton plant and thus it shows its involvement in flowering time and floral organ regulation in cotton plant (Cheng et al., 2021). The GhSOC1 may also bind with GhSPL3 and GhSPL18 and regulates flowering time with respect to photoperiodic pathway and gibberellins signals (Zhang et al., 2015). Studies reveal that GhSPL3 directly regulates the meristem floral genes GhLFY, GhAP1 and GhFUL of the cotton (Yamaguchi et al., 2009).

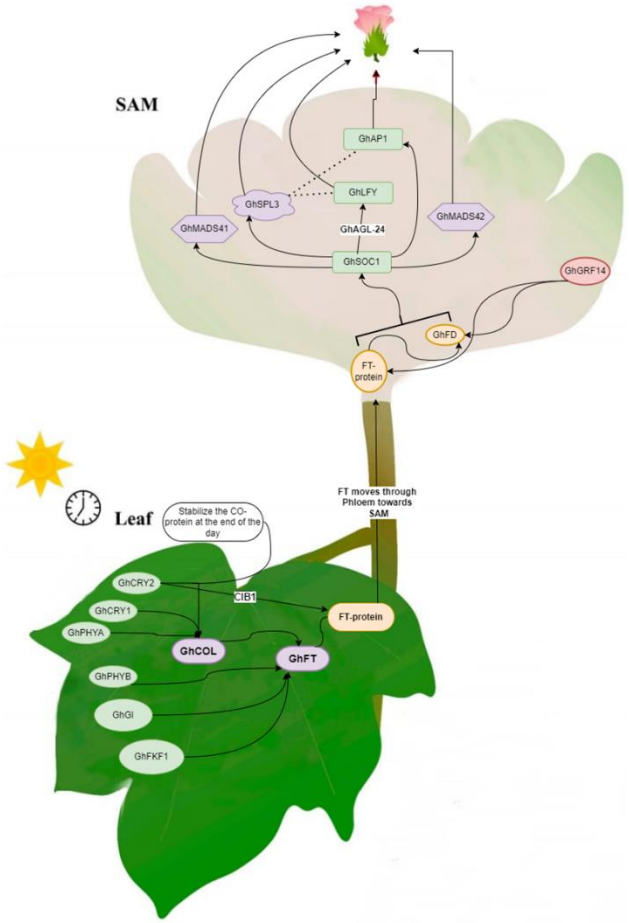

Fig. 7: The pathways of floral transition (flowerings) in cotton. Many photoreceptor and circadian clock regulatory components regulate the GhFT gene transcription. The GhFT-protein (after translation and post transnational process) moves towards shoot apical meristem (SAM) where it interacts with GhFD. The GhGRF14 also interacts with FT and FD in the cotton. The FT-FD complex regulates the expression of GhSOC1 that then regulates many flowering genes like GhMADS41, GhMADS42, GhSPL3, APITALA, LEAFY. All these genes regulate the flowerings in cotton.

GhAAI

The AAI is the large gene family which encodes three domains I.e. trypsin α-amylase domain, hydrophobic seed domain, and LTP2 domains. This gene family involved in vegetative as well as reproductive growth of plants (Tuo et al., 2023). Such as the GhAAI66 was involved in flower development because high transcriptome level of this gene was found in flower. Other genes from the same family like GhAAI2, GhAAI8, GhAAI18, GhAAI65, GhAAI81 was found in ovule of the cotton flower indicating its role in ovule development. Studies also reveal that expression of GhAAI66 was regulated by phytohormonal treatments. It integrates flower signaling pathways like gibberellins and jasmonic acid pathway (Qanmber et al., 2019).

GhPIF

Phytochrome interacting factors (PIFs) regulates the processes like flowerings, seeds germination,

circadian rhythm, shade avoidance etc. (Sharma et al., 2023). In cotton plants, the PIFs have APA and APB motifs through which they regulate phytochrome-A and phytochrome-B (Kaeser et al., 2023). The GhPIFs shows dual response in cotton by promoting and inhibiting the floral growth. Such as in abiotic stress conditions, the GhPIF4 expressed in anthers of the flowers in response to high temperature and this expression cause anther indehiscence and also reduce pollen activity (Zhao et al., 2024). GhPIF4 was also found at shoot tips and in different floral organs abundantly and its suppression can suppress the reproductive growth of cotton. During hot conditions the GhPIF4a regulates the flowerings of cotton by binding with GhFT and the concentration of GhPIF4a/GhFT complex increase with the increase in temperature (Liu et al., 2023).

GhVIN

Cotton male and female fertilities are highly affected by vacuolar invertase (VINs) genes (Wang and Ruan 2016). Invertase are the compounds that hydrolyzes sucrose into glucose and fructose (Wang et al., 2015). As sucrose is the major photosynthetic compound and translocated at non-photosynthetic sites of the plants like roots and reproductive sites. Sucrose is degraded into fructose and glucose by sucrose synthase and sucrose invertase pathways and used in plant for growth and developmental processes (Yoon et al., 2021). The invertase module can be

Table 3: The expression and functions of different cotton flowering genes that involved in the floral development of cotton plant.

Flowering genes	Expression and Functions
GhLFY-like	Flowering initiation at shoot apex during early stages of floral bud development
GhAGL19-like	At early stages of floral bud development
GhCESA-like	Cell wall formation and modification during the early stages of floral bud development
GhEXPBI-like	Cell wall formation and modification during the intermediate stages of floral bud development
GhPMEI-like	Expresses in flower organs like stamen, petal, carpel, sepal during the late stages of floral development
GhNAP-like	During early stages of floral development
GhAP3-like	Intermediate stages of floral development
GhPABP-like	Intermediate stages of floral development
GhLAP5-like	Expressed in different floral organs like stamen, petal sepal during the late stages of floral organ development
GhLAP6-like	Expressed in different floral organs like stamen, petal, carpel, sepal during the late stages of floral organ development
GhPrx-like	Show its expression during intermediate stages of floral development
GhMSI-like	Expressed in different floral organs like stamen, petal, carpel, sepal during the late stages of floral organ development
GhRPD3	Involved in bud differentiation in the early stage of cotton flowering
GhMADS1	It highly expressed in the petals of flowers and also expressed in other floral organs such as stamens and ovules
GhMADS3	Show its expression in stamens and carpels in the wild type cotton
GhMADS7	Involved in the regulation of anther development
GhMADS9	Involved in the regulation of anther development
GhMADS11	Highly expressed in petals and ovules
GhMADS12	Highly expressed in petals and stamens
GhMADS22	Show its expression at shoot apex during floral bud development and also expressed in sepals and bracts of the cotton flower. Its expression dominates in the petals of flower
GhMADS23	Show its expression at shoot apex during floral bud development and also expressed in sepals and bracts of the cotton flower. It can delay floral organ senescence and abscission, improve resistance and also promote flowering
GhSOC1-like	Regulates the transcription of GhLFY
GhAAI2	Involved in the development of ovules
GhAAI8	Involved in the development of ovules
GhAAI18	Involved in the development of ovules
GhAAI65	Involved in the development of ovules
GhAAI66	Involved in cotton flower development
GhAAI81	Involved in the development of ovules
GhVIN	Increase the fertilities of both male and female reproductive organs
GhmiRNA57	Regulates the floral organ development and numbers of ovules in flower by interacting with SPL
GhPS1	Involved in petal development
GhSPL3	Promote flowerings by gibberellin signals and photoperiodic pathway, directly regulates the expression of AP1, FUL and LFY
GhSPL18	Promote flowerings by gibberellin signals and photoperiodic pathway
GhPIF4	In response of high temperature, the GhPIF4 can reduce the pollen activity by affecting anthers. While it also promotes reproductive growth of cotton in the same high temperature conditions
GhPIF4a	Regulates the flowerings by binding with GhFT in hot conditions

classified according to their sub-cellular locations such as cytoplasmic invertase (CIN) (Lou et al., 2007), cell wall invertase (CWIN) (Liao et al., 2020) and vacuolar invertase (VIN) (Slugina et al., 2017). By silencing the vacuolar invertase genes in cotton (GhVIN), it show bad effects on plants like it lost male and female fertilities, seeds unviability, growth repression at filial tissues and block cotton fiber initiation (Wang et al., 2014). These cotton plants were unable to have pollination because of spatially unmatched development between stamen and pistil (or delay in the release of pollens). Because of poor pollen viability, there's also a fertilization failure. While the over-expression of vacuolar invertase genes in cotton (GhVIN) can change these negative affects into positive affects like increase male and female fertility etc. (Xu et al., 2019); Lu et al., (2017).

GhPS1

The GhPS1 is specifically expressed in the petals of cotton flower (Shi et al., 2009). The GhPS1 encodes PGIP (poly-galacturonase inhibitor-like proteins) with its special LRR (leucine rich repeat) domain (Hou et al., 2015). The translation protein of GhPS1 present in the cytoplasm and on the cell membrane also. The expressional product of GhPS1 was continuously up-regulated with the development of petals and its concentration started to decrease with the senescence of petals which shows its involvement in the cotton flower petal development. It has also been proved that GhPS1 is sensitive to temperature as its concentration decreased with the decrease in temperature.

GhmiRNA157

The over-expression of GhmiRNA157 can suppress the cell proliferation and cell elongation which results in the small flower organs, fever ovules (Arora et al., 2021). The average ovules number in a normal ovary of cotton is thirty which can vary from plant to plant and external conditions. The GhmiRNA157 regulates MADS-box genes and auxin signal transduction by targeting SPL genes. So the GhmiR157/SPL complex control the flower growth (Liu et al., 2017).

MADS-Box Genes

The GhMADS1 were expressed in petals, stamens, ovules but most dominantly expressed in the petals of the cotton flower. The GhMADS3 was expressed in the wild type cotton mainly in the stamens and carpels (Guo et al., 2007), GhMADS7 and GhMADS9 regulates the development of anthers of the cotton flowers (Shao et al., 2010), GhMADS11 expressed in petals and ovules while GhMADS12 in petals and stamens (Wang et al., 2011). Some other MADS-box genes like GhMADS22 and GhMADS23 belonged to subgroup genes FUL/AP1/SQUA of cotton (*G. hirsutum*). the expression of these two genes were noted at shoot apex by gibberellic acid. They also expressed in bracts and sepals of the cotton flowers. The GhMADS23 expression dominates in the petals of the cotton flowers than GhMADS22. The over-expression of GhMADS22 can delay floral organ senescence, abscission, improve resistance and promote flowering in cotton plants (Zhang et al., 2013).

Conclusion

Gossypium hirsutum is a tetraploid short day photoperiod plant. However, the cultivated or upland cotton is insensitive to photoperiod. The transition from vegetative to reproductive state is very complicated in *G. hirsutum* because multiple networks of structural and regulatory genes participate in this process. This floral transition initiates by external (light, temperature etc.) and internal (hormonal changes, age factor etc.) factors and generates a floral response in cotton plant. This floral transition is mainly divided into three parts I.e. inputs, circadian clock regulation and output. The photoperiodism is the first stage of this transition that is regulated by light from the external environment. The photoreceptor is one of those that senses light intensity and photoperiod (light-time) and generate response in the plant according to it. The red and far-red photoreceptor such as PHYA, PHYB, PHYC, PHYE are present in cotton. Among of these photoreceptors, PHYA is light unstable means show its response in the absence of light. But PHYA has its role in the floral transition as it helps to stabilize the concentration of CO-proteins in plant, which is the key regulator of floral transition. Blue light photoreceptor CRY1 and CRY2 also involves in the CO-protein stabilization. The GhCRY2 interact with CIB2 and this complex helps to transcribe GhFT that further transcribe GhFD at shoot apical meristem of cotton. The other photoreceptor like PHOTOTROPHINS helps to secure chlorophyll pigments from high intensity blue light and also place this chlorophyll to absorb maximum light in the case when low intensity of light is available for cotton plant. In this way, photoreceptor senses external light conditions and generates responses inside cotton plants according to these environmental messages.

These photo sensory messages are very essential in the plants who follow photoperiodic pathway from vegetative to reproductive transition. The photoreceptor has two main regions in their structures. One is photo sensory region (chromophore) through which plant senses environmental light conditions and the other is protein or coding region through which responses and changes are produced inside the cotton plants. The messages from photoreceptor regulates the circadian clock regulators. Many circadian clock regulatory factors such as GhLUX1, GhELF3, GhGI, GhFKF1, GhCOLs, GhGRFs, CYCLING DOC FACTORS and many mores that are present in cotton plant and regulated by external light source (normally sunlight). Many photoreceptor genes such as GhPHYA, GhPHYB, GhPHYC, GhPHYE, GhCRY1, GhCRY2, GhPHOT1, GhPHOT2 etc. generates responses/changes/factors that regulates the photo-circadian clock regulatory

components. The activation and expression of these circadian clock regulatory components is the second and important part of floral transition as it activates and regulates the expression of FLORAL MERISTEM IDENTITY GENES.

The GhFT is the most important gene because it comprises most of the part of florigen. The GhFT express in the leaves of the cotton and after transnational and post-transnational modification, the GhFT-protein moves towards the shoot apical meristem (SAM) where it interact and regulates the expression of GhFD. The expression of GhFT is regulated by many transcription factors and genes. For example, the genes like GhGRF14, GhCOL1 positively regulates the flowerings in cotton. While the genes like GhTFL1, GhFUL2, GhGRF3, GhGRF6, GhGRF9, GhGRF15 negatively regulate the flowerings in cotton plant.

The flowerings signals started to arise from the leaves of the cotton plants, once the positive environment for floral transition is established inside the cotton plant. The signals arise mostly from leaves and show its structural or phenotypically expression at shoot apex where floral meristem identity genes form floral organs. The axillary bud primordia receive these signals at shoot apical meristem. The axillary bud primordia receive two types of signals in cotton plants for its further transition. One is vegetative signals which results in the formation of leave primordia on the branches of cotton and the other is floral signals which ends up with flowerings on the branches of cotton plant and later it will produce cotton fiber.

The floral bud is appeared on the shoot apex which passes from different developmental stages and form a cotton flower on the branches of cotton plant. The developmental stages of cotton floral bud are divided into three main stages I.e. early flowering stage, intermediate flowering stage and late flowering stage. During the early flowering stage, the formation of stamen primordia, petal and sepal can be seen. During intermediate stage of flowering, the differentiating archesporial cells, ovule primordia and anther primordia is observed. Microsporogenesis of anthers also begins from this stage. The late floral developmental stages further continuous to the rest of the floral parts. The development of both male and female reproductive parts I.e. anthers and ovule respectively, further divided into many (about eleven) developmental stages. Many genes participate in floral organ developments such as GhLFY, GhLAP5, GhLAP6, GhPS1, GhAAIs, GhVINs, MADS-box gene family and many more as shown in Table 3. however, the mechanism of flower development is still unclear in cotton. The floral model of cotton needs more research to clarify the pathways and mechanism of cotton floral development.

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