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REVIEW **Open Access**

An overview of pigment gland morphogenesis and its regulatory mechanism

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Abstract

Cotton has enormous economic potential, providing high-quality protein, oil, and fibre. But the comprehensive utilization of cottonseed is limited by the presence of pigment gland and its inclusion. Pigment gland is a common characteristic of *Gossypium* genus and its relatives, appearing as visible dark opaque dots in most tissues and organs of cotton plants. Secondary metabolites, such as gossypol, synthesized and stored in the cavities of pigment glands act as natural phytoalexins, but are toxic to humans and other monogastric animals. However, only a few cotton genes have been identified as being associated with pigment gland morphogenesis to date, and the developmental processes and regulatory mechanism involved in pigment gland formation remain largely unclear. Here, the research progress on the process of pigment gland morphogenesis and the genetic basis of cotton pigment glands is reviewed, for providing a theoretical basis for cultivating cotton with the ideal pigment gland trait.

Keywords Cotton, Pigment gland morphogenesis, Transcriptional regulation, Terpenoids biosynthesis

Background

Cotton belongs to the genus *Gossypium* in the family Malvaceae and is the leading natural fibre crop worldwide (Huang et al., 2021; Wen et al., 2023). Cottonseed, treated as a by-product in cotton production, can be reprocessed into cottonseed oil, cotton meal, cottonseed husks, and cotton linters, etc., involving food, feed, chemical, pharmaceutical, and other fields (Sunilkumar et al., 2006; Rathore et al., 2020; Gao et al., 2022). Nowadays, nearly 90% of cottonseed is used to produce cooking oil and animal feed, as it is an excellent source of high-quality protein and oil (Gao et al., 2022; Wen et al., 2023). However, the gossypol deposited in cottonseed pigment glands must be chemically removed during this process due to its toxicity to humans and other monogastric animals, which greatly increases the cost of cottonseed processing and further leads to a waste of resources (Tian et al., 2018; Rathore et al., 2020; Lin et al., 2023b).

Pigment glands are one of the major characteristics of *Gossypium* genus and its relatives, and are considered as protective structures formed during evolution (McMichael, 1960; Lin et al., 2023b). The pigment glands in cotton own a unique capacity to synthesize and store secondary metabolites (Gao et al., 2020; Huang et al., 2021). Its inclusions, including gossypol, hemigossypolone, heliocides, and other terpenoids, contribute to the natural resistance to insects and pathogens, such as *Helicoverpa armigera* and *Verticillium dahlia* (Williams et al., 2011; Tian et al., 2018; Lin et al., 2023a, 2023b). Therefore, the study of the morphogenesis and genetic mechanism of cotton pigment glands, the metabolic pathways of inclusions such as gossypol, and their interrelationships have

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always been regarded as the research hot spots (Liu et al., 2010; Lin et al., 2023a; Sun et al., 2023; Wen et al., 2023). The objective of this review is to summarize the morphogenesis and genetic mechanism of cotton pigment glands, and to provide a theoretical basis for developing new cotton varieties that can take into account efficient cotton production and cottonseeds utilization.

Diversity of cotton pigment glands

Pigment glands, also known as "gossypol glands" because of the deposited gossypol and its derivatives, are distributed in most tissues and organs of cotton plants, including stems, leaves, seeds, petals, boll shells, etc. (Fryxell, 1965; Gao et al., 2020). In general, the pigment glands appear as visible dark opaque dots, but diverse colors appear in different tissues by microscopy (Fig. 1) (Ji, 1980; Liu et al., 2010; Zhao et al., 2019). The distribution of pigment glands in cotton plants is also diverse, and is affected by genotypes, plant individuals, organ or tissue sites, growth environment, and developmental period (Mohan et al., 1992). Similarly, the diversity of pigment gland sizes has been revealed, which affected by genotypes and organ or tissue sites. The pigment glands on boll shell typically have the largest size, while the comparatively smallest size is on the cottonseeds (Liu et al., 2017).

According to the morphology of pigment glands, cotton can be roughly divided into four categories, namely glanded cotton, glandless cotton, cotton with glandless-seeds but glanded-plant, and cotton whose seeds are glanded without gossypol. At present, almost all the main cotton cultivars are glanded, including *G. hirsutum* and *G. barbadense*. The pigment glands of diverse sizes and densities appear in all parts of the glanded cotton plant except pollen and seed coat, among which cottonseeds have the highest density (Sunilkumar et al., 2006; Zhao et al., 2019; Long et al., 2023). The second category, glandless cotton is characterized by the absence of pigment gland and gossypol in the whole plant and cottonseeds (Zhao et al., 2019; Huang et al., 2021). The first natural glandless mutant in upland cotton was discovered by McMichael (1959), and the majority of commercial ultra-low gossypol germplasm lines belong to this category (McMichael, 1959). However, due to the low gossypol content in cotton plants, the resistance to diseases and insect pests is weakened, and the yield is reduced, which limits the use of this category in production (Rathore et al., 2020; Zhang and Wedegaertner, 2021). The third category, the cotton with glanded-plant and glandless-cottonseeds were found in several wild diploid Australian cotton species, as represented by *G. bickii* and *G. australe* (Fryxell, 1965; Cai et al., 2020; Sheng et al., 2023). The dormant cottonseeds of these cotton species are glandless and gossypol-free. After seed imbibition, the pigment glands are gradually presented and the plants are normal glanded (Sheng et al., 2023; Sun et al., 2023). This characteristic of gradual formation of pigment glands during seed germination is also coined "delayed pigment gland morphogenesis" (Zhu et al., 1999a; Zhu et al., 2001). And the fourth category, the cotton whose cottonseeds have sparse pigment glands with undetectable gossypol, includes only two wild cotton species, *G. stocksii* and *G. somalense* (Xiang et al., 1993). Akin to delayed pigment gland morphogenesis, masses of pigment glands develop and form with gossypols accumulated during seeds germination (Ding et al., 2004). Therefore, it has also been

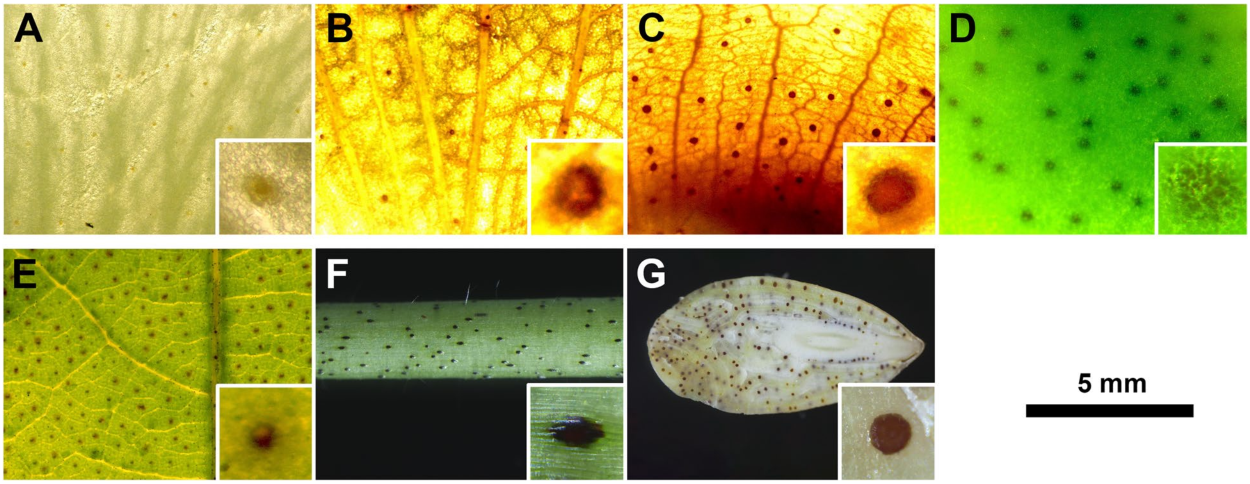

Fig. 1 Morphological characteristics of pigment glands in different organs of glanded cotton. **A**, Petal; **B**, Bract; **C**, Sepal; **D**, Boll shell; **E**, Leaf; **F**, Stem; **G**, Cottonseed

considered as an intermediate transition type between the glanded cotton and the delayed-pigment-gland-morphogenesis cotton (Zhu et al., 1999a; Ding et al., 2004).

The cotton species with this unique trait of delayed pigment gland morphogenesis are of great breeding value in both cottonseed utilization and stress resistance improvement. For this ideal trait, attempts have been made for the interspecific crossing between these delayed-pigment-gland-morphogenesis wild cotton species and tetraploid cultivated cottons. Trispecies bridge crosses have been carried out for the triple allotetraploids (*G. arboreum* × *G. bickii* [2n = 52, $A_2A_2G_1G_1$]) × *G. hirsutum*, (*G. arboreum* × *G. bickii* [2n = 52, $A_2A_2G_1G_1$]) × *G. barbadense*, (*G. herbaceum* × *G. australe* [2n = 52, $A_1A_1G_2G_2$]) × *G. hirsutum*, and (*G. thurberi* × *G. sturtianum* [2n = 52, $D_1D_1C_1C_1$]) × *G. hirsutum* (Zhang et al., 1993; Zhu et al., 1995; Vroh Bi et al., 1999a, 1999b; Zhu et al., 1999b, 2004, 2005; Liu et al., 2015). Meanwhile, the synthetic hexaploid avenues have also been attempted through the amphidiploid (*G. hirsutum* × *G. australe* [2n = 78, $AADDG_2G_2$]) or (*G. hirsutum* × *G. bickii* [2n = 78, $AADDG_1G_1$]) consecutively backcrossing with upland cotton (Chen et al., 2014; Tang et al., 2018). However, due to the difficulty in interspecific introgression, this ideal trait has not been successfully transferred into cultivated cottons for commercial production.

Cotton pigment glands morphogenesis

Cotton pigment gland morphogenesis is a complex process that remains elusive, and the study on the development of pigment glands started from the last century (Stanford et al., 1918; McMichael, 1960). In general, the pigment glands are supposed to originate from clusters of meristem beneath the epidermis (Liu et al., 2010). And it is reported that mature pigment glands form a cavity surrounded by radially flattened cells, in which the residual cell walls are still evident (Stanford et al., 1918; Yatsu et al., 1974). However, there have been two diverse views for interpreting the morphogenesis of pigment glands, i.e., schizogenous process and lysigenous process. According to Tschirch (1906) and Liu et al. (2010), the pigment gland cavities are formed through schizogenous process, in which special cells are separated and metabolites appear between these cells. Conversely, more research papers supported the lysigenous process hypothesis, which is a typical form of autophagic programmed cell death (Stanford et al., 1918; Yatsu et al., 1974; Dangl, 2000; Liu et al., 2010; Sun et al., 2023). Cytology studies have shown that the initial gland primordium cells are constantly developing and differentiating into central enlarged secretory cells and multiple layers parenchyma distributed around the cavity. Subsequently, cell walls of the internal cells begin to degrade, forming a cavity. And the autolysis of secretory cells by programmed cell death releases secretion products, including gossypol, into the cavity. Later, with the tangentially elongation of pigment gland cells and the nternal cells completely broken down, the cavity of the pigment glands become more evident. Ultimately, the mature cotton pigment glands consist of multiple layers of parenchyma, monolayer of secretory cells in the outer, and the residual of apoptotic cell in the inner cavity (Yatsu et al., 1974; Liu et al., 2010; Sun et al., 2023).

The time point of cottonseed pigment gland morphogenesis is distinct in each category of cotton. Observation of tissue structure of dormant mature cottonseeds, germinating cottonseeds, and embryos during anthesis showed that pigment gland morphogenesis of most glanded cotton, such as upland cotton, occurs in embryos at approximately 18 days post-anthesis (Jan et al., 2022; Sheng et al., 2023). As for the delayed-pigment-gland-morphogenesis cotton, only clusters of initial cells distinguishable from other cells, called gland primordium cells, appear in the mature seeds, and pigment glands morphogenesis can be observed in germinating seeds (Zhu et al., 1999a; Zhu et al., 2001). For example, the dormant cottonseeds of *G. bickii* are glandless with only partial gland primordium cells, and the pigment gland structures become visible in the cotyledons at approximately 36 h after seed imbibition (Sheng et al., 2023; Sun et al., 2023). As for *G. stocksii*, both the pigment gland cavities and the gland primordium similar to those in *G. bickii* can be observed in the mature seeds (Ding et al., 2004).

Genetic basis of cotton pigment glands

Genetically, pigment gland formation in cotton is complex with numerous regulatory factors. Research on the basis of pigment gland formation in the cotton began following the discovery of the glandless mutants "Hopi Moencopi" since the 1950s (McMichael, 1954, 1959). The first recessive genetic locus, gl_1, was identified as responsible for the pigment gland formation on the stems, petioles, hypocotyl, and boll shells (McMichael, 1954). Subsequently, two relatively independent recessive genes, gl_2 and gl_3, were identified from the essentially glandless plants isolated from the cross of Hopi Moencopi and Acala (McMichael, 1960). Double recessiveness of these two loci ($gl_2gl_2gl_3gl_3$) led to a completely glandless phenotype in *G. hirsutum*, and the presence of the dominant alleles (Gl_2 or Gl_3) led to the presence of pigment glands with the display of variable pigment gland distribution patterns according to genotypes (McMichael, 1960; Miravalle, 1962; Lee, 1965). Besides these, three additional relatively weak alleles were also identified in upland cotton, among which gl_4 and gl_5 reduced only a tiny fraction of pigment glands, while gl_6 had similar but slighter effects to gl_1 (Lee, 1962, 1965; Murray, 1965; Lusas et al., 1987).

In addition to the six independent loci mentioned above, breeding and genetic studies have also identified the multiple alleles with similar effects at major loci, namely gl_2^{arb} in *G. arboreum*, gl_3^{thur} in *G. thurberi*, gl_3^{dav} in *G. davidsonii*, gl_3^{rai} in *G. raimondii*, and gl_2^{b} and gl_3^{b} in *G. barbadense* (Bell et al., 1977). Genetic analysis indicated that the glanded leaves and low gossypol content seed character of the mutant Xiang X9628 are controlled by two pairs of recessive duplicate genes, gl_2 and the new multiple allele gl_3^{n} (Zhang et al., 2001). And the delayed pigment gland morphogenesis trait of the new upland cotton germplasm, named ABH-0318, was controlled by the interaction of the genes located at two loci, gl_3 from *G. hirsutum* and dominant multiple allele Gl_2^{b} derived from *G. bickii* (Zhu et al., 2001; Zhu et al., 2004). In addition, a single dominant glandless allele of Gl_2, Gl_2^{e}, was discovered from the entirely glandless line Bahtim 110 developed from the progeny of *G. barbadense* Giza 45 treated with radioactive phosphorous (^{32}P), and it showed the epistatic effect on Gl_3 (Afifi et al., 1966; Kohel et al., 1984).

Since then, these unique glandless germplasms have been used to breed many glandless cultivars of both *G. hirsutum* and *G. barbadense*, and to develop genetic populations to map the genes responsible for pigment gland morphogenesis (Yu et al., 2000; Cheng et al., 2016; Ma et al., 2016; Zang et al., 2021). The gene underlying Gl_2^{e} was the first identified gene through fine genetic mapping by cross populations, and was named *Gossypium Pigment Gland Formation* (*GoPGF*), which encodes a basic helix-loop-helix domain-containing transcription factor (Cheng et al., 2016; Ma et al., 2016). Sequence alignments of glandless mutants showed that the amino acid change from alanine to valine at residue 43 resulted in the dominant Gl_2^{e}, whereas the single T or A was inserted into *GhPGF_A12* (*GoPGF* genes in the chr. A12, Gl_2) or *GhPGF_D12* (*GoPGF* genes in the chr. D12, Gl_3) introduced premature translation termination, resulting in the recessive gl_2 and gl_3 alleles (Ma et al., 2016). The significant role of *GoPGF* in the pigment gland morphogenesis has also been further confirmed and low expression level of this gene by silencing or knockout resulted in the completely glandless phenotype in cotton (Ma et al., 2016; Janga et al., 2019; Li et al., 2021).

Three *cotton gland formation* (*CGF*) genes, *CGF1*, *CGF2*, and *CGF3* (synonym of *GoPGF*) were identified by comparative transcriptome analysis on glandless near-isogenic cotton lines, of which *CGF1* encoded a bHLH transcription factor had a dramatic effect on the pigment gland density and *CGF2* encoded a NAC transcription factor impacted on gland density and terpenoids in the leaves of mutants (Janga et al., 2019). Moreover, another newly identified gland-associated gene, *GauGRAS1* in *G. australe*, was confirmed to be responsible for stem pigment gland formation, and the homologous gene in *G. hirsutum*, named *Gossypium Stem Pigment Gland Forming Gene* (*GoSPGF*, gl_1), has also been identified by genetic mapping (Cai et al., 2020; Zang et al., 2021). Recently, single-cell transcriptomic analysis has been used to reveal the gene regulatory network in pigment gland morphogenesis and has released some novel transcription factor, for instance, *GbiERF114*, *GbiZAT11*, and *GbiNTL9* in *G. bickii*, and *GhJUB1* (synonym of *CGF2*) in *G. hirsutum* (Long et al., 2023; Sun et al., 2023; Zhang et al., 2023). To date, the identified regulators of pigment gland formation are all transcription factors, consisting of the core *GoPGF* and the genes regulated or affected by it (Table 1, Fig. 2) (Ma et al., 2016; Janga et al., 2019; Cai et al., 2020; Gao et al., 2020; Wang et al., 2021; Yi et al., 2022; Zang et al., 2021; Sun et al., 2023; Wen et al., 2023).

The inclusions of cotton pigment gland cavities

The pigment gland cavities of cotton accumulate a large number of secondary metabolites that can protect plants against pathogens, insects, and herbivores. Beside the common non-volatile terpenoids such as gossypol, heliocides H1 to H4, and hemigossypolone, cotton plants also release a complex blend of volatile terpenes stored in pigment glands, including α-pinene, (E)-β-ocimene, myrcene, and (E)-β-caryophyllene (Opitz et al., 2008; Lin et al., 2023a). All these terpenoids in cotton pigment gland are biosynthetically related, and there are several regulators governing terpenoid biosynthesis (Lin et al., 2023a; Zhang et al., 2023). CDN ((+)-δ-cadinene synthase), CYB706B1, DH1 (short-chain alcohol dehydrogenase 1), CYP82D113, CYP71BE79, SPG (specialized glyoxalase I), CYP736A196, 2-ODD-1 (2-oxoglutarate/Fe (II)-dependent dioxygenase 1), and GhDIR4/5/6 were identified as enzymes of gossypol biosynthesis (Tian et al., 2018; Lin et al., 2023b). *GaWRKY1* has been isolated from *G. arboreum* and identified to participate in the regulation of sesquiterpene biosynthesis in cotton which affects the expression of key synthase gene *CAD-1* (Xu et al., 2004). Moreover, comparative transcriptomes of several glanded and glandless cultivars identified a MYB transcription factor, named *Cotton Gland Pigmentation 1* (*CGP1*), as a regulator of sesquiterpene phytoalexin biosynthesis, which controlled by interacting with GoPGF to form a heterodimer in the nucleus (Gao et al., 2020). The recent study of *G. bickii* has shown that *GbiCYP76B6*, regulated by *GoPGF*, affects the sesquiterpene biosynthesis in cotton (Sheng et al., 2023). And single-cell transcriptomic analysis of cotton leaves revealed two novel genes, *GoHSFA4a* and *GoNAC42*, operating

Table 1 The research progress in pigment gland genes

Gene	Source species	Gene clone	Encode TF	Function in pigment gland	References
gl_1 (*GoSPGF*)	*G. hirsutum*	Yes	GRAS	Responsible for the glandless phenotype on the stems, petioles, hypocotyl and boll shells	McMichael, 1954
gl_2, gl_3	*G. hirsutum*	Yes	bHLH	Responsible for the completely glandless phenotype in all parts of cotton	McMichael, 1960
gl_4	*G. hirsutum*	No	-	Weak alleles, reducing pigment glands in all parts of cotton	Lee, 1962
gl_5	*G. hirsutum*	No	-	Weak alleles, reducing pigment glands in all parts of cotton	Lee, 1962
gl_6	*G. hirsutum*	No	-	Similar but slighter effects to gl_1	Murray, 1965
gl_2^{arb}	*G. arboreum*	No	-	The multiple allele of gl_2 with similar function in *G. arboreum*	Bell et al, 1977
gl_3^{thur}	*G. thurberi*	No	-	The multiple allele of gl_3 with similar function in *G. thurberi*	Bell et al., 1977
gl_3^{dav}	*G. davidsonii*	No	-	The multiple allele of gl_3 with similar function in *G. davidsonii*	Bell et al., 1977
gl_3^{rai}	*G. raimondii*	No	-	The multiple allele of gl_3 with similar function in *G. raimondii*	Bell et al., 1977
gl_2^b, gl_3^b	*G. barbadense*	No	-	The multiple allele of gl_2 and gl_3 with similar function in *G. barbadense*	Bell et al., 1977
gl_3^n	*G. hirsutum*	No	-	Responsible for the character of glanded plants and glandless cottonseeds	Zhang et al., 2001
Gl_2^b	*G. bickii*	No	-	Responsible for the delayed pigment gland morphogenesis trait	Zhu et al., 2004
Gl_2^e (*GoPGF*)	*G. barbadense*	Yes	bHLH	Dominant glandless allele, responsible for the completely glandless phenotype in all parts of cotton. CRISPR/Cas9-mediated knockout of *GoPGF* genes resulted in the completely glandless phenotype in cotton. Silencing *GoPGF* using a seed-specific promoter led to a glandless phenotype with an ultra-low gossypol content in the cottonseeds	Afifi et al., 1966; Ma et al., 2016; Gao et al., 2022
CGF1	*G. hirsutum*	Yes	bHLH	Reducing the number of pigment glands in all parts of cotton	Janga et al., 2019
CGF2 (*GhJUB1*)	*G. hirsutum*	Yes	NAC	Reducing the gland density in all parts of cotton. CRISPR/Cas9-mediated knockout of *CGF2* genes reduces gland density and terpenoids in the leaves of mutants	Janga et al., 2019; Long et al., 2023
CGF3	*G. hirsutum*	Yes	bHLH	Synonym of *GoPGF,* responsible for the completely glandless phenotype. CRISPR/Cas9-mediated knockout of *CGF3* genes results in glandless phenotype	Janga et al., 2019
GauGRAS1	*G. australe*	Yes	GRAS	Homologous gene of *GoSPGF*, responsible for stem pigment gland formation	Cai et al., 2020
GbiERF114	*G. bickii*	Yes	AP2/ERF	Affecting pigment gland formation and reducing the pigment gland density	Sun et al., 2023
GbiZAT11	*G. bickii*	Yes	C2H2	Affecting pigment gland formation and reducing the pigment gland density	Sun et al., 2023
GbiNTL9	*G. bickii*	Yes	NAC	Affecting pigment gland formation and reducing the pigment gland density	Sun et al., 2023

downstream of *GoPGF*, which can regulate biosynthesis of volatile terpenes and non-volatile terpenoids (Lin et al., 2023a).

Among them, gossypol is the most primary ingredient stored in the cavities of pigment glands, which is used as a symbol of inclusions for the controversial relationship with pigment glands. According to the physiological and biochemical phenotypes observed in glanded cotton, gossypol content was highly correlated with the density of pigment glands. Usually, the size and density of

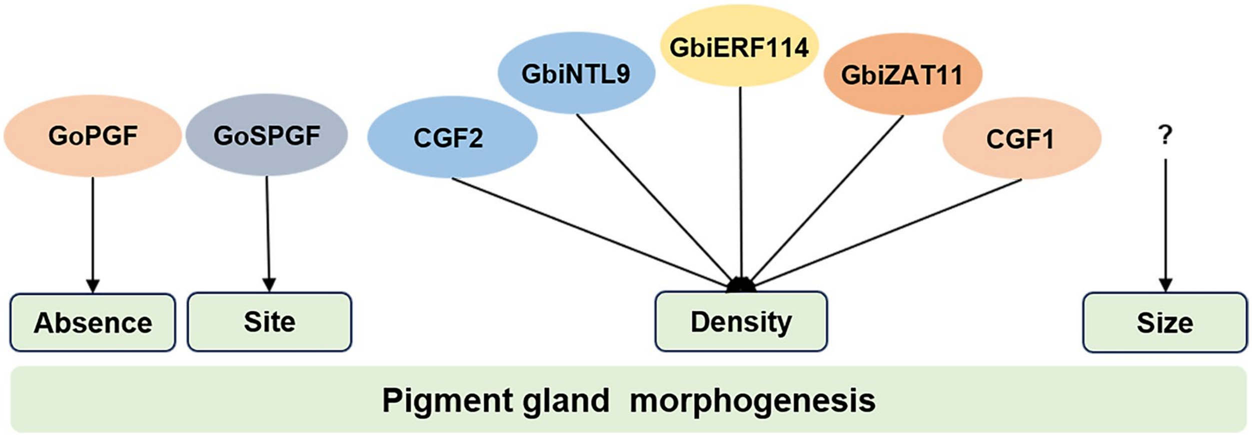

Fig. 2 Regulation of pigment gland morphogenesis. GoPGF protein, as a master regulator, controls the presence or absence of pigment glands. Other transcription factors are responsible for various aspects of pigment gland morphogenesis. Different colors represent different types of transcription factors. Abbreviations: GoPGF, *Gossypium* Pigment Gland Formation; GoSPGF, *Gossypium* Stem Pigment Gland Forming; CGF2, cotton gland formation 2; GbiNTL9, *Gossypium bickii* NAC TRANSCRIPTION FACTOR-LIKE 9; GbiERF114, *Gossypium bickii* ETHYLENE RESPONSE FACTOR 114; GbiZAT11, *Gossypium bickii* ZINC FINGER OF ARABIDOPSIS THALIANA 11; CGF1, cotton gland formation 1

pigment glands are often used as the indicators to weigh the gossypol content in cotton breeding (Singh et al., 1972; Wilson et al., 1976). However, there are exceptions in some wild cotton species, namely *G. stocksii* and *G. somalense*, whose cottonseeds have sparse pigment glands with gossypol undetectable(Xiang et al., 1993). Furthermore, several studies have shown that regulatory genes of pigment gland formation were also able to significantly affect gossypol accumulation, while blocking gossypol biosynthesis by gene silencing or knockout had less effect on pigment gland formation (Sunilkumar et al., 2006; Ma et al., 2016; Janga et al., 2019; Cai et al., 2020). Interestingly, this complex relationship can be explained by recent investigations of pigment gland cell in cotton leaves. Through single-cell transcriptome analysis, it was confirmed that the terpenoid synthetic genes were specifically and highly expressed in pigment gland cells, which further revealed that pigment glands were the synthetic sites of terpenoids rather than just the storage sites of gossypol produced by the pigment-gland-independent pathway in roots (Long et al., 2023; Sun et al., 2023; Zhang et al., 2023). Thus, terpenoids synthesis is one of the unique functions of pigment gland cells, but the terpenoids content in cavities is also affected by transported substances synthesized in cotton roots (Zhao et al., 2020; Zhang et al., 2023).

Future perspectives

With the advancement of high-throughput sequencing technology and gene editing technology, especially the quick growth of single-cell sequencing technology in recent years, more and more regulators linked to pigment gland formation will be discovered and identified, which will help to elucidate the molecular mechanism of pigment gland formation (Lin et al., 2023a; Long et al., 2023; Sun et al., 2023). On this basis, genetic engineering methods are used to further generate cotton varieties with diverse pigment gland types required for production despite the drawbacks of traditional breeding, such as the long cycle and hardship in breaking the negative chain (Khan et al., 2023). Currently, there are several objectives for cotton pigment gland breeding, and the majority of research focuses on using molecular cloning and genetic engineering techniques to produce glandless cotton, so that cottonseeds can be directly consumed (Sunilkumar et al., 2006; Li et al., 2021; Zhang et al., 2021; Gao et al., 2022). Or contrarily, cultivation of cotton with high density or large size of pigment glands with high content of effective inclusions can enhance the resistance of cotton plants to diseases, insect pests, and pathogens, thereby increasing the cotton yield (Lin et al., 2023b). The long-term goal of future research should be to reveal the mechanisms underlying the pigment glands morphogenesis and inclusions biosynthesis and storage, to develop novel cotton varieties that account for efficient cotton production and cottonseeds utilization. Breeding strategies such as genetic engineering are bound to advance the breeding process of cotton pigment glands and promote the sustainable development of the cotton industry.

Conclusions

Pigment glands are one of the most crucial traits in cotton breeding, and extensive research has been conducted on the morphological differences, morphogenesis, distribution, and genetic mechanism of pigment glands. Up to now, several genes regulating development of pigment glands and accumulation of gland inclusions have been identified, such as *GoPGF*, *CGF1*, and *CGF2*, among which *GoPGF* is the most critical one for development of pigment glands. Thus, it would be a step further strategy to identify the potential transcriptional regulatory mechanisms of pigment glands using technology with rapidly developing, and to breed ideal cotton varieties that take into account efficient cotton production and cottonseeds utilization by genetic engineering.

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Authors' contributions
Zhu SJ and Zhao TL conceptualized the project. Yang P, Han YF, Li HZ, Sun DL, and Chen JH contributed to discussion. Sun Y wrote the manuscript draft, and Zhao TL revised it. All authors read and approved the final manuscript.

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All the authors and co-authors have given their consent for publication.

Competing interests
All authors declare no competing interests.

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