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REVIEW ARTICLE

Cotton fibre development: Genes and physiological determinants of fibre length

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Abstract

Cotton fibres, single-celled extensions of the seed epidermis, progress through a series of developmental stages. This review explores fibre developments' genetic and physiological components, focusing on factors that affect fibre length. An attempt has been made to summarize the evolution of cotton species, highlighting the transition from wild to cultivated types and the selection for improved fibre traits. The stages of fibre development–initiation, elongation, secondary wall synthesis and maturation, as well as the roles of specific genes and physiological determinants governing fibre length during these processes, are discussed. The prospects for improving cotton fibre length to meet the industry standards, supported by the wealth of research information generated, are also outlined.

Keywords

cotton fibre development; expansin; fibre elongation; fibre initiation; fibre length; turgor

Introduction

Cotton, known for its high cellulose content, is Earth's most abundant natural polymer, emphasizing its invaluable role in various industries (1). Accounting for nearly 50% of all the fibres used, cotton dominates the textile sector with its longer, stronger and finer fibres, making it highly desirable for spinning industries (1). Statista data for 2022/2023 (2) estimates a global cotton production of approximately 118.3 million bales (175 kg each). India emerged as a critical player in this domain, contributing 316.57 lakh bales. However, according to reports from the Cotton Corporation of India (2022-23 provisional)(3), 25 lakh bales of cotton are being exported, indicating excess output from local demand. The import of 12 lakh bales of cotton, likely extra-long staple (ELS) cotton, indicates an unmet demand for premium-quality cotton in India. This shows a need for improvement in domestic cotton production, possibly in the area of quality enhancement to reduce reliance on imports for ELS cotton.

The genus *Gossypium,* which comprises 50+ species, is a part of the *Malvaceae* family that produces seed trichomes. It belongs to a small tribe *Gossypieae,* which includes only nine genera (4). These genera comprise eight monophyletic diploid groups with genomes A to K from different geographical locations (5) and one monophyletic tetraploid group with genome AD (6). The cultivated species include *Gossypium herbaceum* and *G. arboreum,* diploid Old World cottons with an A genome, *G. hirsutum* with an AD_1 genome and *G.*

barbadense with an AD_2 genome. The evolution of the A genome diploid, *G. herbaceum* and subsequent natural hybridization, followed by a polyploidization event after the trans-oceanic dispersal of the A genome species with the D genome species, *G. raimondii*, led to the evolution of the AD genome (7-9). Wild diploids produce varying degrees of seed pubescence, generally shorter, i.e., 1-10 mm (9). Polyploidization events have enabled humans to select for better fibre quality (10).

Interestingly, the fibre traits of allotetraploids have been enhanced compared to those of their AA and DD genome relatives, primarily due to intense selection pressure on fibre quality traits (11). The observed interspecific differences in fibre length are mainly attributed to variations in the absolute fibre elongation rate and the duration of the elongation phase, with minimal influence from the fibre initiation phase in which epidermal cells protrude to form fibre initials (12). It is critical to understand the importance of fibre quality over sheer yield due to its direct impact on market value. Therefore, understanding the physical, physiological and genetic factors involved in fibre development is imperative for enhancing fibre quality, which is crucial for addressing the needs of sophisticated spinning.

Development of Cotton Fibre: Temporal Transformations and Regulations

The study of cotton fibre development is essential due to its commercial implications. The economic significance of cotton domestication stems from the unique ability of a single epidermal cell on the ovule of the cotton fruit to produce long, solid and single-celled trichomes or hairs (11). The value of cotton is not solely based on the presence of fibre but also depends on its quality, especially in the context of advancements in spinning technologies (13). As a result, breeders now emphasize both fibre quality and yield. The length and quantity of cotton fibres vary among wild and cultivated cotton species. Wild cotton (like *G. davidsonii*, *G. trilobum* and *G. armorianum*) typically has only one layer of fibre and rarely grows more than 1 cm in length (12), while cultivated cotton, including *G. hirsutum* and *G. barbadense,* can reach up to 6 cm in length and contains two layers of fibres: lint, the longer fibre, suitable for textiles and fuzz, the shorter fibres (4,14).

Cotton fibre development occurs in a series of distinct but overlapping stages (Fig. 1.), beginning before anthesis and continuing for approximately 50 days post-anthesis (DPA) (5,12). These stages include fibre initiation, which begins before anthesis, followed by tip refinement at 1-2 DPA and elongation through primary cell wall synthesis (15), which ceases at ~20 DPA in domesticated cotton (12,16,17). At the same time, this process may terminate in wild species as early as 15 DPA (12). Subsequently, secondary wall synthesis occurs, followed by maturation and cell death at ~50 DPA (15). Genetic factors primarily govern fibre length and diameter. In contrast, physiological factors largely influence fibre maturity and are therefore more susceptible to environmental factors like temperature, soil moisture and precipitation (18,19).

Fibre initiation and tip refinement

Approximately one in four epidermal cells in cotton plants protrude to form fibre initials on or near the day of anthesis, signifying the onset of fibre initiation (18,19). Fibre initials emerge through isodiametric diffuse expansion (20) from the epidermal surface and are driven by elevated turgor pressure (15). Cellulose microfibrils and transverse microtubules regulate the extent of diametric growth (20). During this process, fibre initials first appear at the chalazal end on the day of anthesis and gradually progress towards the micropylar end (5,12,21,22). The shape of the fibre initials also varies between species and across days, ranging from short and round to long and pointed forms (5).

On the other hand, fuzz development depends on both the species and variety and is thought to begin a few days after anthesis (23). Fibre growth starts anisotropically within the next 24 hours (22), reaching approximately 80 µm at 2 DPA (19), at which point its blunt tips begin to taper (5,22). Between 1-4 DPA, fibre elongation progresses relatively slowly and steadily, after which the elongation rate doubles (4-5 DPA). By then, the fibre tips have also been established. There are three distinct fibre tips: blunt (hemisphere) and tapered (24), which are apparent and intermingled on the chalazal end at 2 DPA in *G. hirsutum* and the third type, narrow tip present in *G. barbadense*. These fibre tips persist throughout the fibre elongation and secondary wall development phases and are correlated with the diameter of the mature fibre (25). Although these three fibre types have different diameters at 4 DPA, they elongate at a comparable rate (25). Remarkably, *G. hirsutum* exhibits two distinct tip morphologies, resulting in heterogeneous fibres on individual seeds and consequently

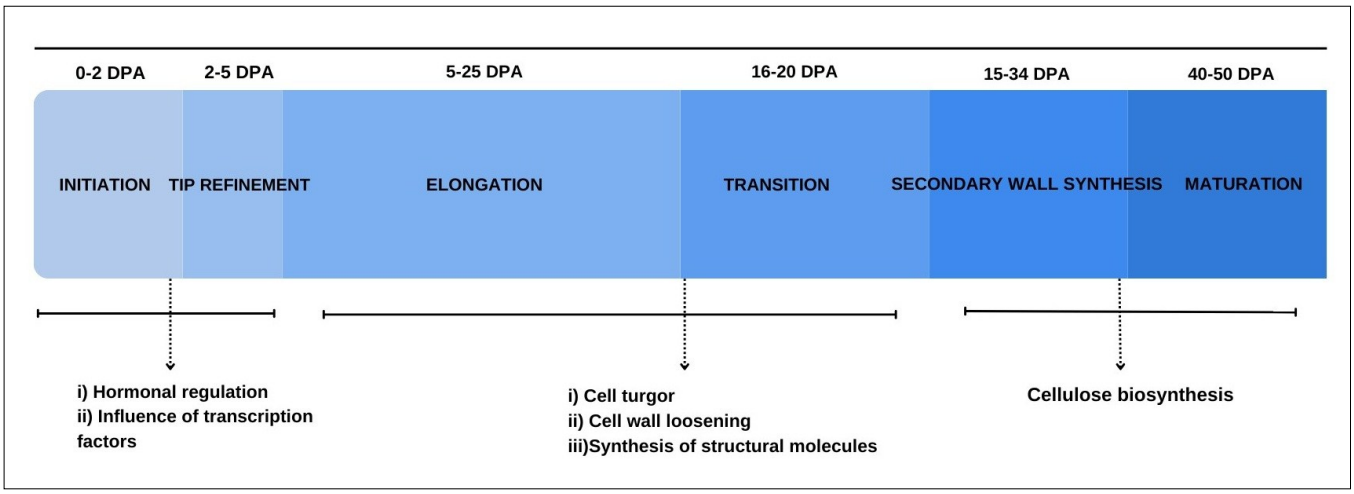

Fig. 1. Developmental phases of cotton fibre along with critical factors for fibre length (DPA: Days Post Anthesis).

produces bolls with slightly varied characteristics. Fibres with hemispherical tips have a twofold larger apical diameter than tapered tips, potentially influencing overall fibre length and strength (24,25). Each ovule undergoes semi-synchronous, dynamic growth, with fibres on chalazal and micropylar ends showing variations in development length. At 4 DPA, the micropylar end has fibres at the initiation and early polar development stages, whereas the long fibres are at the chalazal end (25). It was opined by the researchers that opined that final fibre length varies between species, with *G. hirsutum* fibres reaching 322 µm by 5 DPA (5).

Determinants of Fibre Initiation: Fibre initiation involves a complex integration of hormonal regulation (26), relative oxygen species (ROS) signalling and high-level transcription factors, influencing the expression of specific genes that drive fibre initiation. For instance, a critical regulator of cotton fibre initiation and elongation, the transcription factor GhWRKY16, which GhMPK3-1 phosphorylates, is necessary for the transcriptional activation of downstream genes, including those with wide regulatory roles, such as *MYB109* and *MYB25*, in turn influencing the length of the fibre (27). GhWRKY16 also binds to the promoters of other genes, such as *GhHOX3, GhMYB109* and *GhMYB25,* to induce their expression, influencing fibre initiation and elongation (28,29).

As mentioned earlier, fibre initiation is influenced by changes in hormone-regulating genes; auxin plays a crucial role in this process. Auxin accumulates before flowering, peaks at 2-3 DPA, and then progressively decreases (30). It was reported that in addition to the contribution of PIN (PIN-FORMED) genes in fibre initiation, increased expression of *PINa*, *PIN6* and *PIN8* contributes to cotton fibre elongation in *G. hirsutum* (31). Silencing *PIN1a* reduces auxin transport and decreases fibre elongation (32). Furthermore, long-fibre group lines had fewer fibres than the short-fibre group lines, but their fibre length was greater (33). This finding suggests efficient energy distribution in gene transcription may be essential for regulating fibre growth.

Fibre elongation and transition

Fibre elongation commences after tip refinement and culminates with mature fibre length at approximately 14 DPA in wild species and between 18-25 DPA in domesticated species (12,18). The fibre undergoes linear development during this period and produces the primary cell wall. Cotton fibres exhibit diffuse growth and are not tip-growing cells (34). In elite domesticated lines, fibre length can reach up to 6 cm (18) with a peak expansion rate of over 2mm/day in *G. hirsutum* (18).

Various factors facilitate fibre elongation, including primary cell wall composition, turgor pressure, and cytoskeletal organization. For cotton fibre elongation, the cell wall loosens, intense turgor pressure is generated and the cytoskeleton is rearranged (35). The primary cell wall mainly consists of cellulose, pectin and xyloglucan (36). De-esterified pectin is the primary component found in the primary cell walls of cotton fibres during elongation (37), comprising ~25% of the fibre's cell wall (38,39). It may be diminished or absent in non-extendable secondary cell walls (37). Pectic-hemicellulosic primary walls appear as early as 5 DPA (39), with a thin cellulose layer evenly distributed throughout the primary wall, except at the fibre tip, composed primarily of pectinaceous material. Tiny vacuoles in the fibre tip do not overlap with the central vacuole, which occupies much of the fibre length (39). The cotton fibre middle lamella (CFML), a unique adhesive outer layer of the primary wall that is produced during fibre initiation plays a crucial role in organizing fibres during elongation by joining *G. hirsutum* fibres together to form tissue-like bundles (15,40). CFML contributes to the growth of fibres with longer, well-defined bundles and prevents them from elongating in random directions (40). Thus, each locule of cotton boll likely facilitates more than 100,000 fibres in a small area exceptionally due to the ordered packing of fibres (36).

The CFML layer disintegrates during secondary wall formation (~22 DPA), but the inner primary wall layer encircles the protoplast endures (36). Interestingly, elongation in *G. barbadense* can last up to 25 DPA, whereas in *G. hirsutum,* elongation usually ends at 20 to 22 DPA (12,41). The longer time required for *G. barbadense* fibres to elongate than those of *G. hirsutum* fibres is believed to contribute to the superior quality of *G. barbadense* fibres (41). The elongation phase is shorter in wild species, reaching approximately 14 DPA (12). *GhACTI* transcripts reach their maximum length during the fibre elongation phase, supporting the actin cytoskeleton necessary for sustaining and enhancing spatial patterning (42). Expansins, wall-loosening agents involved in fibre expansion, disrupt the noncovalent adhesion of cell wall matrix polysaccharides to cellulose microfibrils (43,44). However, they do not degrade the major polysaccharides of the wall network (45), which is accomplished by pectate lyase (46), as described in the later section.

Fibre Transition: The period when the fibre shifts from elongation to secondary wall synthesis is known as the transition phase. Primary cell wall remodelling and cellulose synthesis are initiated in this transition stage (36). Around 16 DPA, primary cell wall deposition and elongation start to decline, ultimately halting in all the species by 25 DPA, *i.e.,* elongation persists even after secondary cell wall deposition begins. However, it significantly slows down during the transition phase (16-20 DPA) (41,47). The secondary cell wall deposition process, which starts during the transition stage, thickens the fibre over the next 20 to 30 days, resulting in a cell wall composed primarily of cellulose unique among plant cell walls (34).

Determinants of Fibre Elongation for Fibre Length: The elongation of cotton fibre cells is a complex and precisely regulated process involving metabolic pathways, signal transduction and transcriptional regulation (Fig. 2.) (48). The coordinated interplay between these signalling and metabolic pathways governs the intricate process of initial cell elongation and subsequently supports cellulose synthesis (49). Fibre length is determined by both the rate and duration of cell expansion, which is regulated by developmental processes that synchronize the modulation of cell turgor (the driving force behind cell expansion), cell wall loosening and synthesis of structural molecules (44,50,51). Each of these processes is examined in detail in subsequent sections.

Physiology of turgor maintenance in elongating fibres

Cell osmotic pressure, sugars, organic acids and potassium promote horizontal and longitudinal elongation (52). The leading cause of cell turgor in cotton fibres is the influx of water,

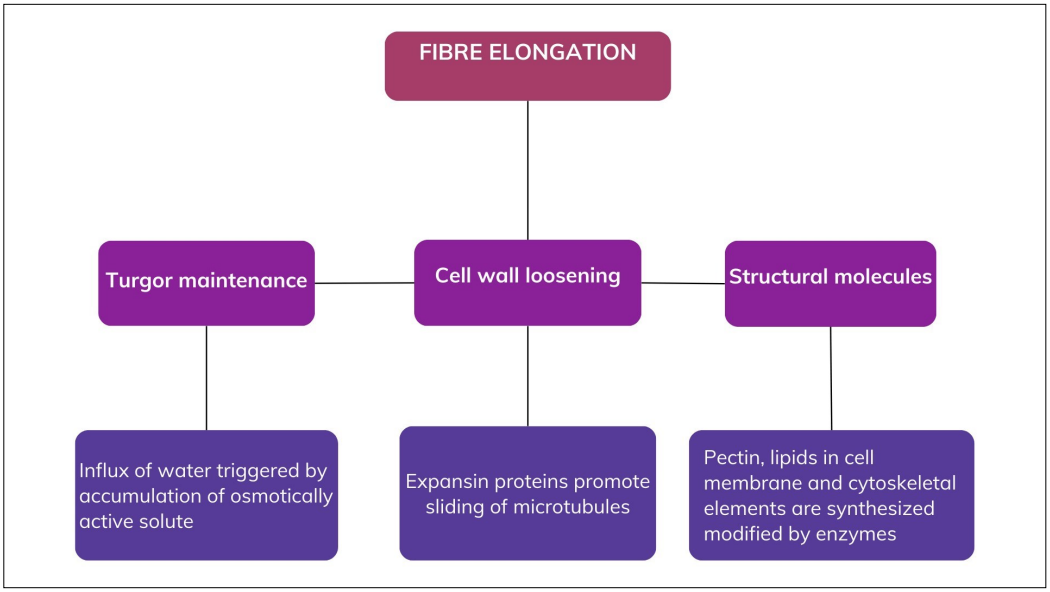

Fig. 2. Overview of the regulation of fibre elongation phase.

which is triggered by the accumulation of osmotically active solutes, primarily hexoses, potassium (K^+) and malate (Fig. 3.) (52,53). GhCIPK6 regulates the accumulation of a high concentration of K+ in vacuoles in growing cotton fibres (44,53). A lack of Ca^{2+} may also cause K^+ to accumulate in fibre cells, contributing to cell elongation. The genes encoding xyloglucan endotransglycosylases/hydrolases (XTH), EXP (expansion) and PSK (phytosulfokine) are also significantly activated by Ca^{2+} shortage (53). PSK may reduce K^+ efflux, promoting fibre cell elongation (54). The high-affinity K^+ absorption gene *GhKT1* is preferentially expressed at 10 DPA during cotton fibre development, coinciding with the transitory closure of plasmodesmata (10-16 DPA) (44). It is anticipated that the lengthier plasmodesmata closure at the fibre base in *G. barbadense* than that in *G. hirsutum* would enable high turgor in *G. barbadense* fibre (55). As noted earlier, the elongation rate of *G. hirsutum* fibres starts to decline sooner than that of *G. barbadense* fibres, possibly due to differences in K^+ homeostasis. This suggests that elongating fibres with enough K^+ maintains osmotic balance and modulates hormone levels (abscisic acid and jasmonic acid) under Ca^{2+} deficient conditions. This promotes cell wall loosening through activation of key genes (*PSK, EXP, XTH*), while *GhCIPK6* (CBL-INTERACTING PROTEIN KINASE 6) facilitates K^+ uptake ensuring sustained fibre elongation and longer fibres (53).

The production of malate and consequently an osmotic potential that propels fibre elongation, is supported by the high phosphoenolpyruvate carboxylase (PEPC) activity in fibres (44). The transcript levels of two significant PEPC genes, *GhPEPC1* and *2*, expressed in cotton fibres, are consistently more important in the rapid elongation phase. PEPC also affects lipid synthesis and other activities potentially leading to fibre elongation (56), i.e., during fibre elongation, when the plasma membrane and tonoplast increase at a high rate, PEPC activity may be necessary for the manufacture of membrane lipids (44).

In higher plants, sucrose is the main byproduct of photosynthesis and is a significant carbohydrate transferred from source to sink tissues via the phloem. The initiation and elongation of cotton fibres have been linked to the sucrose

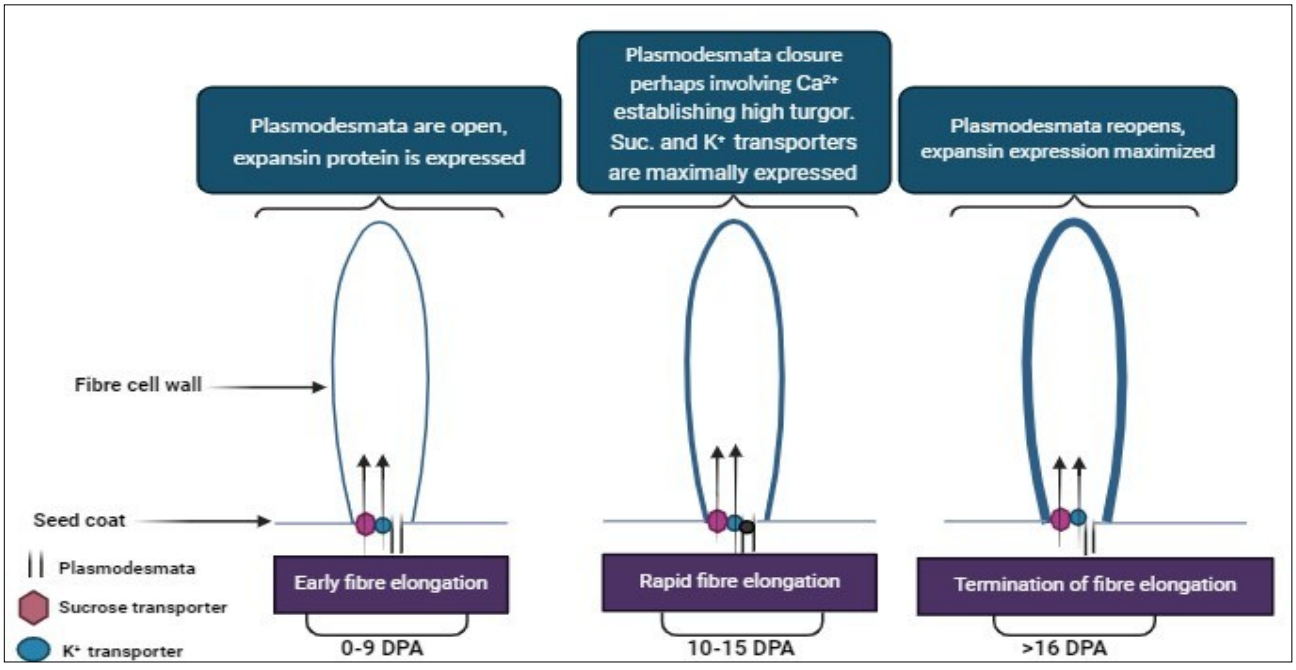

Fig. 3. Regulation of fibre elongation *via* turgor maintenance and expansion proteins.

synthase gene (*Sus*), which influences the partitioning of carbon to cellulose synthesis (57). Conversely, invertase irreversibly hydrolyses sucrose into fructose and glucose (58). In elongating fibres, *GhVIN* activity (a type of invertase) is significantly elevated during the rapid elongation phase. Despite a paradoxical decrease in VIN activity after 5 DPA, it remains approximately 2-fold greater at 10 days than after 15-20 DPA. This finding implies that during the 10-15 DPA period, VIN activity may influence fibre elongation using osmotic control (35).

Physiology of cell wall loosening

At the elongation stage, fibre cell wall looseness is maintained by essential proteins, expansins, endo-1,4-beta-glucanase (44,57) and tubulins (42,59). *EXPA*s produce polysaccharide complexes linking cellulosic microfibrils, such as pectin and xyloglucan (60). At acidic or low wall pH, the cell wall elongation of growing cotton fibre affects enzyme activation. Among the critical pH-sensitive enzymes, expansins and xyloglucan endotransglycosylases/hydrolases (XTHs) are particularly relevant. Expansins are activated in acidic conditions, facilitating the loosening of the cellulose-hemicellulose network in the cell wall, which allows for cell wall extension and fibre elongation. Similarly, XTHs, which catalyze the cleavage and reattachment of xyloglucan chains in the cell wall, are most active at acidic pH, supporting dynamic wall remodelling required for elongation (61).

At the early elongation phase (0-9 DPA), plasmodesmata are open for solute transport, resulting in an acidic intracellular environment (62). At this stage, the *Sus* gene controls sucrose utilization in the cell and expansin genes control the sliding of cellulose microtubules to loosen the cell wall (63). The plasmodesmata close with the maximum intake of ions and sugars in the middle of the expanding phase. This creates intense turgor pressure within the fibre, allowing maximum elongation of up to 16 DPA. Later, the expansion of expansin decreases when the cell wall becomes rigid, preventing further elongation (64).

Synthesis of structural molecules

Pectin, lipids found in cell membranes and cytoskeletal elements are the fundamental substrate for primary cell wall formation. Pectin is produced in the Golgi apparatus, de-esterified and found on the primary cell wall (37). It is modified by enzymes crucial for the elongation of fibres (46,49,65). Pectate lyase (*GhPEL*) is an important agent in fibre cell elongation (46). It is significantly produced during the fibre rapid elongation stage (10 DPA) to accelerate the depolymerization of de-esterified pectin on the primary cell wall for fibre wall loosening (46). Also, *GhKCS* encoding ketoacyl -CoA synthase (KCS) is essential for the synthesis of very long-chain fatty acids (VLCFAs) (26). Sphingolipids, including trihydroxy long-chain bases and saturated VLCFAs, are crucial for fibre elongation because they provide structural components to expand the fibre membrane (66). Additionally, arabinogalactan proteins (AGPs) are prevalent in growing fibres with enhanced expression at 10 DPA and are implicated in fibre elongation.

Regulation of the fibre transition phase: During the transition phase, cotton fibres require turgor-driven cell expansion to ensure a pliable primary wall and facilitate the movement of solutes. *G. barbadense* at 25 DPA exhibits a strong expression of the two novel genes encoding glucan endo-1,3-beta-glucosidase-like protein 4 (E13L3) involved in callose binding activity (41). This leads to regulating plasmodesmata closure *via* increased callose accumulation (44,67). In contrast, several β-1,3-glucanase genes that regulate the opening of plasmodesmata by breaking down callose are expressed at low levels in *G. barbadense* fibres (44). In accordance with the more prolonged fibre elongation stage of *G. barbadense* compared to *G. hirsutum*, these two gene families regulate the length of plasmodesmata closure to maintain high turgor for an extended period.

Secondary wall synthesis and maturation

Cotton fibre mainly consists of α-cellulose with β-1,4-D (+)-glucopyranose building block. The primary cell wall contains less than 30% cellulose, a relatively low molecular weight. It is also composed of noncellulosic polymers, neutral sugars, uronic acid and various proteins. In contrast, the secondary cell wall comprises 100% cellulose, with the highest molecular weight among various plant fibres (1).

Fibre elongation decreases at 17-33 DPA, secondary cell wall synthesis begins (~17 DPA), and the transition period ends (36,68). Approximately 14-16 DPA upregulates genes involved in secondary cell wall biosynthesis. Cellulose synthesis increases at approximately 14 DPA and by 25 DPA, fibres in all species would have reached secondary cell wall thickening. β-1,4-glucan chains are organized into cellulose microfibrils, which make up the secondary cell wall and influence the properties of the cell wall (68). The cellulose microfibrils are arranged helically around growing fibres with periodic reversals in the deposition angle. Therefore, fibres become twisted in reversal regions (18), which is said to be correlated with fibre strength (69). Although fibre initiation is independent of pollination/fertilization (23), these processes may influence elongation and maturation (39).

Additionally, secondary wall development is associated with the location of the seed in the locule (70) and the position of the fibre on the seed (71). Fibre maturation stops at 40-60 DPA, depending on the genotype and environmental conditions. The fibre maturity represents the degree of fibre cell wall thickness indirectly assessed by micronaire measurements (68). As the fibre matures, it twists and compresses into a bean-shaped cross-section. The fibre cells then die, dry out and the bolls dehisce.

Regulation of secondary wall synthesis

The metabolic pathways active during fibre elongation, particularly secondary metabolism, are repressed in this phase. The hydrolysis of noncellulose oligo- and polysaccharides, as well as fatty acids, is upregulated simultaneously. The pathway that yields carbohydrates and converts them into recyclable cellulose is preferred. During the secondary cell wall synthesis stage, this coordinated regulation directs carbon flux toward cellulose biosynthesis (49). The protein WLM1a, preferentially expressed in cotton fibre cells and its stem, has dual functions and nuclear or cytoplasmic localization. This gene is expressed during elongation and secondary wall formation phases (6-24 DPA) and plays a role in crosstalk between these stages. At the

elongation stage, it binds to the actin cytoskeleton to bundle them (cytoskeletal organization), which is actively involved in the intracellular transport of cell wall components and membrane during fibre elongation. This is advantageous for rapid fibre elongation. Later, when the fibre elongation is arrested and there is a ROS burst, WLIM1a moves to the nucleus, binds to PAL-box genes involved in phenylpropanoid synthesis and promotes the synthesis of lignin/lignin-like phenolics (transcriptional regulation), which are essential for the secondary wall formation (54). Additionally, the overexpression of *WLM1a* results in a noticeable increase in fibre length (36,72). Several factors involved in different phases of fibre development are also presented in Table 1.

Conclusion

This review examines the genetic and physiological factors influencing cotton fibre length, encompassing the developmental stages from initiation through elongation to fibre maturation. It also emphasizes the critical understanding of fibre development stages, pinpointing specific genes and physiological elements crucial for fibre length improvement. This knowledge is essential for breeding strategies aimed at augmenting fibre length, thereby enhancing the market value of cotton. Insights from this review hold significant practical implications, particularly in addressing the growing demand for premium-quality cotton, such as ELS cotton, in India. By focusing on quality enhancement through targeted breeding programs, domestic cotton production can be optimized to meet market demands, reduce reliance on imports and strengthen the textile industry's economic foundation.

Table 1. Key factors and their functions involved in different phases of cotton fibre development

Genes Regulating Fibre Length	Functions	Fibre development phase	Reference
GhMYB109	Encodes an R2R3 MYB transcription factor	Fibre Initiation and elongation	(29,73)
GhACT1	Maintain actin cytoskeleton's integrity	Fibre elongation	(42)
GhADF1	An ADF regulating actin cytoskeleton's dynamic	Elongation and secondary cell wall formation	(74)
Gh_D03G1338	-	Fibre elongation	(75)
PIN family	-	Fibre elongation and elongation	(31)
GhPRE1	A PRE gene in hormonal regulation or cell wall modification	-	(76)
ERF1	Ethylene signalling pathway	Fibre elongation	(33)
TUA2	Microtubule organization	Fibre elongation	(33)
TUB1	Microtubular structure	Fibre elongation	(33)
PER64	Modulation of cell wall structure and response to oxidative stress	Fibre elongation	(33)
MIR160a_A05	Downregulates ARF17 and several GH3 genes	Fibre elongation	(77)
Ghir_D10G011050	-	Fibre elongation	(78)
CB5	Electron transport in various metabolic pathways	Fibre elongation	(79)
EB1C	Microtubule organization	Fibre elongation	(79)
GRF5 of miR396 gene family	Growth regulating factor 5 gene	Fibre elongation	(80)
GhCaM7-like gene	CaM gene in calcium signalling pathways	Fibre elongation	(81,82)
QTL *qFL-c10-1* *qFL-chr1*	Harbour genes associated with fibre quality	-	(80)
GhMYB7	A MYB transcription factor in cell differentiation and secondary metabolism	Fibre elongation	(83)
GhMYB25 and *GhMYB25-like*	Secondary metabolism	Initial differentiation and early elongation	(83)
GhMYB46	Secondary cell wall biosynthesis	Late elongation	(83)
GhDEL65	A bHLH transcription factor	An early stage of fibre elongation	(83)
GhPEL76	Encodes pectate lyase	Fibre elongation	(46,8)
GhLTPG1	LTPs in the transport of fatty acids	Rapid fibre elongation	(83)
GhFIM2	FIMBRIN(FIM) proteins for the organization of actin filaments	Fibre elongation	(83)
GhEXPA8	An Expansin involved in loosening cell walls	Rapid fibre elongation	(83)
GAST1-like	Regulates H_2O_2 levels	Fibre elongation	(84)
Cop1/BONZAI	Regulates H_2O_2 levels	Fibre elongation	(84)
Pex1	Regulates H_2O_2 levels	Fibre elongation	(84)
GhPRP5	Interacts with auxin-responsive family protein	Fibre initiation	(85)
CotAD_28189	Encodes a D-cysteine desulfhydrase	-	(85)
CotAD_02795	Encodes thaumatin-like protein (TLP).	Secondary cell wall synthesis	(85)
GhARF2 and *GhARF18*	Auxin response factors	Initiation	(86)
GhAPX1	ROS scavenging	Fibre elongation	(86)

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None

Authors' contributions

All authors contributed to the study's conception and design. MM and AS wrote the first draft of the manuscript and all authors commented on previous versions. AS supervised the study. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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