Cotton fibers are single-celled extensions of the seed epidermis. They can be isolated in pure form as they undergo staged differentiation including primary cell wall synthesis during elongation and nearly pure cellulose synthesis during secondary wall thickening. This combination of features supports clear interpretation of data about cell walls and cellulose synthesis in the context of high throughput modern experimental technologies. Prior contributions of cotton fiber to building fundamental knowledge about cell walls will be summarized and the dynamic changes in cell wall polymers throughout cotton fiber differentiation will be described. Recent successes in using stable cotton transformation to alter cotton fiber cell wall properties as well as cotton fiber quality will be discussed. Future prospects to perform experiments more rapidly through altering cotton fiber wall properties via virus-induced gene silencing will be evaluated.

Keywords: cellulose, cotton fiber, elongation, xyloglucan
FIGURE 1 | A representation of the progression of cotton fiber development. The “stem” indicates the fastest developmental timeline when plants are grown under warm conditions. “Branches” show DPA, with associated images of fiber. Cryo-field-emission SEM of (A) fiber initials on the ovule surface (bar = 10 μm); (B) twisting and elongating 3 DPA fibers (bar = 100 μm); (C) CFML stretched between two 3 DPA fibers (bar = 4 μm); (D) ordered bundles of fibers inside the boll (bar = 100 μm). Differential interference contrast micrographs indicating microfibril angle (as highlighted by arrows) in fiber at (E) 16 DPA and (F) 20 DPA (bars = 10 μm). TEM fiber cross-section shows (G) an early stage of secondary wall thickening (bar = 300 nm); and (H) a more advanced stage of secondary wall deposition (bar = 1 μm). (I) Mature cotton boll and (J) cross-section of mature fiber viewed in the light microscope. SCW, secondary cell wall. Re-published with permission from The Cotton Foundation (http://www.cotton.org/foundation/index.cfm; Stiff and Haigler, in press).

and/or cellulose (β-1, 4-glucan) synthesis. Drug treatments of cotton fiber showed that cellulose fibril orientation, but not cellulose synthesis itself, depended on microtubules (Seagull, 1993), which was confirmed by live cell imaging in Arabidopsis (Paredes et al., 2006). Biophysical analyses on cotton fiber revealed cellulose IV in primary walls (Chanzy et al., 1978), helped to define cellulose Iα and cellulose IIβ cellulose allomorphs (Atalla and Vanderhart, 1984), and demonstrated the higher molecular weight of secondary wall versus primary wall cellulose (Timpa and Triplett, 1993).
For secondary wall cellulose synthesis, cotton fibers adopted the genetic program of scleranchyma cells of the plant body (e.g., xylem tracheary elements and interfascicular fibers) while shunting down the synthesis of the matrix polysaccharides and lignin (Haigler et al., 2009; Betancur et al., 2010). This finding was surprising given that cotton fibers are morphologically classified as trichomes. Nonetheless, the apparent orthology of genes required for secondary wall synthesis in arabidopsis scleranchyma cells are up-regulated at the onset of cotton fiber secondary wall deposition (Haigler et al., 2005, 2009; Al-Ghazi et al., 2009; Singh et al., 2009a; Hinchliffe et al., 2010). In contrast, genes encoding the secondary wall-related CESA isoforms are not up-regulated in arabidopsis leaf trichomes as shown by qRT-PCR, microarrays, analysis of CESA promoter:GUS reporter genes in transgenic arabidopsis, and observation of thick trichome walls in arabidopsis lines with non-functional secondary wall cellulose synthases (Betancur et al., 2010). This result is consistent with the contrast between the nearly pure cellulose in cotton fiber secondary walls versus a blend of traditionally defined primary and secondary wall components (including cellulose, pectin, mannan, and lignin) in mature trichome cell walls (Marks et al., 2008). Comparisons of developmentally regulated gene expression sets confirmed the traditional primary wall-related characteristics of arabidopsis leaf trichomes as contrasted with traditional secondary wall-related characteristics of cotton fiber at the onset of wall thickening (Betancur et al., 2010). The xylem-derived genetic program adopted by cotton fiber was present at the base of the land plant lineage with little change since that time (Haigler et al., 2009; Hinchliffe et al., 2010; Zhong et al., 2010), also reflected in comparisons of gene expression within and between Gossypium species (Al-Ghazi et al., 2009; Rapp et al., 2010). Scleranchyma cells, not leaf trichomes, provide the best analogies in the model plant arabidopsis for cell wall thickening in cotton fiber. This illustrates the flexible use of a “plant cell wall toolbox” to generate diverse cell walls particularly suited for the purpose (Betancur et al., 2010).

COTTON FIBER CELL WALL COMPOSITION

Cotton fiber cell wall composition changes dynamically throughout development. In young fiber between 0 and 2 DPA: (a) a pectin-rich, xyloglucan-depleted outer sheath develops; (b) an epitope is lost that is characteristic of (1–6)-β-D-galactan carrying arabinose (possibly contained in situ within arabinogalactan protein); and (c) an epitope appears that is characteristic of (1–4)-β-D-galactan, one of the possible side chains of rhamnogalacturonan I (Vaughn and Turley, 1999; Bowling et al., 2011). Also by 2 DPA, the synthesis of a cotton fiber middle lamella (CFML) begins. This thin adhesive outer primary cell wall layer is enriched in fucosylated and non-fucosylated xyloglucan and homogalacturonan with no or relatively low esterification. The CFML serves to join adjacent fibers into tissue-like bundles that become highly organized and tightly packed within the confined boll space (Singh et al., 2009a). The inner cotton fiber primary wall contains ~22% crystalline cellulose fibrils surrounded by xyloglucan and pectin (Meinert and Delmer, 1977; Singh et al., 2009a). Glycome profiling of fiber wall extracts with numerous monoclonal antibodies recognizing plant polysaccharide epitopes (Pattathil et al., 2010) showed that xylan and acetylated mannose also exist in cotton fiber (Haigler et al., in preparation). Genes encoding expansin, a cell wall loosening protein, are expressed during cell wall elongation and associated with QTLs related to fiber length (Harmer et al., 2002; An et al., 2007). At the transition stage between primary and secondary wall deposition, transcriptionally-regulated cell wall degradative enzymes break down the CFML so that fibers are released as individuals – a phenomenon correlated with decreases in primary wall-related sugars, up-regulation of cell wall hydrolases, and reduction of pectin and xyloglucan molecular mass as secondary wall synthesis begins (Meinert and Delmer, 1977; Tokumoto et al., 2002, 2003; Guo et al., 2007; Singh et al., 2009a).

A distinct transition stage between primary and secondary wall deposition occurs in cotton fiber. During the transition, a unique “winding” cell wall layer, analogous to the S1 layer in wood fiber, is laid down over several days (Seagull, 1993). Fiber strength increases substantially at this time although wall thickening is minimal (Hsieh et al., 1995; Hinchliffe et al., 2011), presumably due to the differently oriented cellulose microfibrils in the winding layer compared to the primary wall. The winding layer may also fuse the primary and secondary cell walls together. Other developmental changes also occur at the transition stage: microtubules rearrange to support the changed direction of cellulose fibril deposition in the cell wall; respiration rate declines temporarily; concentrations of some metabolic sugars change; cellulose synthesis rate increases along with an increase to ~35% (w/w) in cellulose content; the CFML degrades; and the level of callose peaks within the cotton fiber cell wall. At the onset of secondary wall thickening, the rate of cellulose synthesis increases again and both microtubules and cellulose fibrils adopt a steep helix relative to the fiber axis (Meinert and Delmer, 1977; Malby et al., 1979; Seagull, 1993; Martin and Haigler, 2004; Guo et al., 2007; Singh et al., 2009a; Abidi et al., 2010). The cotton fiber secondary wall ultimately becomes 3–6 μm thick.

CELL WALL-BASED CONTROLS OF COTTON FIBER MORPHOGENESIS AND QUALITY

Through comparing different cotton genotypes and/or experiments with cotton ovule/fiber culture, insights are emerging about how cell walls control cotton fiber morphogenesis and quality. As predicted given the positive correlation between pectin supply and cell expansion in plants (Boyer, 2009), signaling pathways (related to ethylene and C24:0 lignoceric acid) stimulate gene expression related to pectin biosynthesis as part of promoting fiber elongation (Qin et al., 2007; Pang et al., 2010). A family of recombinant inbred lines between Gossypium species with lower and higher fiber quality showed a correlation between expression of a pectin methyltransferase gene and fiber quality (Al-Ghazi et al., 2009). Increasing the amount of de-esterified homogalacturonan reduced fiber elongation in transgenic cotton: up to 14% shorter fiber developed on plants with lower activity of pectate lyase, which can degrade de-esterified homogalacturonan (Wang et al., 2010a). In keeping with the above correlations, probing wild-type fiber cross-sections and cell wall extracts with antibodies provided evidence for increased de-esterification of homogalacturonan near the end of fiber elongation (Singh et al., 2009a). These data are
cotton fiber elongation (Lee et al., 2010). Similarly, XTH activity
or field conditions. Therefore, the transfer of xyloglucan chain
about twofold higher XET activity and 15–20% longer fiber com-
transgene and increased fiber length. The transgenic plants had
GhXTH1
mote fiber elongation (Cosgrove, 2005 ). Consistent with this
possibly increase the plasticity of the primary wall and pro-
mote fiber elongation (Cosgrove, 2005). Consistent with this
prediction, transgenic cotton plants constitutively over-express-
GhXTH1 showed a positive correlation between inheritance of the
transgene and increased fiber length. The transgenic plants had
about twofold higher XET activity and 15–20% longer fiber com-
pared to wild-type cotton or null segregants under greenhouse or
field conditions. Therefore, the transfer of xyloglucan chain ends
between molecules was predicted to be a limiting factor for
cotton fiber elongation (Lee et al., 2010). Similarly, XTH activity
was lower in a short fiber mutant compared to wild-type cotton
(Shao et al., 2011).

The timing of the transition to secondary wall deposition is: (a)
affected by temperature and exogenous hormones in vitro (Roberts
et al., 1992; Singh et al., 2009b); (b) differs between cultivars grown
in the greenhouse (Abidi et al., 2010); and (c) correlates with dif-
ferences in fiber bundle strength in two near-isogenic lines grown
in the field (Hinchliffe et al., 2010). Field studies of the two near-
isogenic lines showed that the time of onset of the transition stage
was determined by the accumulation of a minimal number of heat units. Earlier entry into the transition stage resulted in higher
fiber bundle strength, for reasons that remain to be discovered
(Hinchliffe et al., 2011), and it is correlated with shorter fiber in
transgenic cotton over-expressing GhFPN2, a profilin gene. Pro-
filin is an actin bundling protein, and GhFPN2 is normally highly
expressed between 15 and 24 DPA (Wang et al., 2010b). Correlating
with these results, transgenic cotton plants with down-regulated
expression of GhADF1, encoding an actin-depolymerizing fac-
tor, had a heritable increase in fiber length (Ye et al., 2011). Under salt stress, higher cellulose content occurred in trans-
genic cotton over-expressing mustard annexin compared to wild-
type, and genes encoding sucrose phosphate synthase, sucrose
synthase, and cellulose synthase were up-regulated in leaves and
fiber (Dviya et al., 2010). These results correlate with increased
fiber cellulose content when transgenic cotton over-expressing spinach sucrose phosphate synthase was grown in the growth
chamber under cool night conditions (Haigler et al., 2007).

*VIRUS-INDUCED GENE SILENCING AS AN EFFICIENT TOOL FOR TESTING COTTON GENE FUNCTION*

Knock-down of gene expression through virus-induced gene
silencing (VIGS; Robertson, 2004) can occur without stable trans-
formation, which is inefficient in cotton (Wilkins et al., 2004). In
VIGS experiments, a modified virus transiently down-regulates
(silences) a plant messenger RNA (mRNA; Ruiz and Baulcombe,
1998). During viral infection, the plant produces small-interfering
RNAs (siRNAs) complementary to the viral genome (Hamilton
and Baulcombe, 1999). These siRNAs bind to homologous tar-
get mRNAs and ultimately prevent translation of the target gene
(Brodsky et al., 2008). When a fragment of a plant gene is
inserted into a VIGS vector, both the viral transcripts and the
targeted plant transcript(s) are silenced (Kumagai et al., 1995).
Down-regulation of the targeted gene will ideally lead to a pheno-
type that reveals the gene’s function. For a possibly redundant gene
family, a conserved fragment can be used to potentially knock-
down the expression of several genes and increase the chances of
observing a phenotype. VIGS has been successfully used in Nic-
tiana benthamiana to produce phenotypes by silencing cell wall
biosynthetic genes (Burton et al., 2008; Hoffmann et al., 2004; Ahn
et al., 2006; Zhu et al., 2010).

Two VIGS vectors have been developed for cotton: one from a
DNA virus (Cotton leaf crumple virus, CLCV; Turtle et al.,
2008) and another from a broad-host-range RNA virus (Tobacco
rattle virus, TRV; Ve et al., 2010; Gao et al., 2011). These VIGS vec-
tors are introduced into the plant by either agrobacterium (TRV
and CLCV) or particle bombardment (CLCV only). Following
inoculation, silencing initiates between 7 and 14 days post infec-
tion (dpi, TRV) or by 21 dpi (CLCV). The extent of silencing
from both CLCV and TRV is inversely associated with growth
temperature (Fu et al., 2006; Turtle et al., 2008). Neither CLCV-
VIGS nor TRV-VIGS produced completely uniform silencing in
all cultivars (Idris et al., 2010; Gao et al., 2011). Silencing a visi-
ble marker, such as PDS or GFP, along with the target gene may
be necessary in some cases to facilitate phenotyping (Quadrami
et al., 2011), and experiments are ongoing to employ this strat-
egy in cotton fiber (Tuttle, 2011). There are two strategies for
achieving VIGS in cotton fiber: (1) plants are inoculated early
followed by translocation of the vector or siRNAs to the devel-
oping cotton fibers; or (2) isolated ovules are inoculated and
followed by translocation of the vector or siRNAs to the devel-
oping ovules (Ye et al., 2010). Under salt stress, higher cellulose content occurred in trans-
genic cotton over-expressing mustard annexin compared to wild-
type, and genes encoding sucrose phosphate synthase, sucrose
synthase, and cellulose synthase were up-regulated in leaves and
fiber (Dviya et al., 2010). These results correlate with increased
fiber cellulose content when transgenic cotton over-expressing spinach sucrose phosphate synthase was grown in the growth
chamber under cool night conditions (Haigler et al., 2007).

**FUTURE PROSPECTS**

Virus-induced gene silencing technology will synergize with cot-
ton genome sequencing (Chen et al., 2007; Paterson et al., 2010;
see http://www.phytozone.net/cotton.php) to make cotton fiber
In summary, key elements are converging to make cotton fiber one of the most useful systems for cell wall and cellulose research. Further analysis of cotton fiber cell walls is relevant to improvement of this important textile fiber and to creating the next generation of crop plants for optimized production of biofuels and biomaterials.

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Cotton fiber cell walls

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