Chapter 23

LINT DEVELOPMENT

Edmond A.L. DeLanghe
Katholieke Universiteit Leuven
Heverlee, BELGIUM

INTRODUCTION

When a cotton flower blooms, a number of cells in the outer epidermal layer of the ovules show a bulging of the outer wall. This is the onset of a very fast, 1000- to 3000-fold, elongation leading to gigantic tubular hair cells up to 6 cm long. They consist of a very thin cuticulum, a thin primary wall remarkable for its combination of strength and extreme extension, a thin cytoplasmic layer and an enormous vacuole. During a second period, the vacuole will shrink progressively while, at the inside of the primary wall, a mass of almost pure cellulose is deposited as a secondary wall. By the time of boll maturation the secondary wall will normally fill the major part of the cell volume, leaving the lumen, the small central cavity, containing the remainder of the cytoplasm and the vacuole. As the boll opens, quick desiccation of the tubular cells occurs. They collapse longitudinally, and assume a ribbonlike form with special twists called convolutions. This is the cotton fiber.[1]

The development of the cotton fiber has been explained many times since Balls (1915). For the state of knowledge of cotton and its cellulose at the end of the 1960's, refer to two excellent reviews by Rollins (1968a,b).

The unique, hence non-representative, form of the cotton fiber is probably just the reason why, in the past, surprisingly little research had been directed toward understanding how the cotton fiber cell synthesizes cellulose and incorporates it into a cell wall (Westafer and Brown, 1976). But during the last decade, physiological research on the developing cotton fiber has contributed in a large measure to better understanding of several fundamental aspects of cell differentiation, cell expansion and cellulose synthesis.

[1]Since this chapter is not dealing with the development of the so-called "fuzz-fibers", the word "fiber" is exclusively used in the present context as an alternative expression for "lint fiber" or "lint". The word "fiber" stands also in this text for the corresponding cell during its development into the real fiber, the latter being the harvested product of the mature cotton boll. Wherever it is felt necessary, exact expressions such as "elongating epidermal cells" are preferred.

On the other hand, since the cotton fiber plays an important role in the textile industry, the technological study of its physical and mechanical properties began during the 19th century (Bowman, 1882). That research produced a universally recognized terminology for the characterization of the cotton fiber as it is available on the market in baled cotton. Despite long-established cooperation between cotton breeders and fiber technologists, it remains difficult to "translate" some technological properties in terms of morphogenetic processes. The recent advances in physiological research on cotton fiber development will probably enable the cotton grower, the breeder and the agronomist to better control development with a view to desired properties in the future.

FIBER INITIATION

With the exception of stomatal cells, mainly located at the chalazal end, the cells of the outer epidermal layer of a cotton ovule are cuboidal during the last days before anthesis. They are either in a state of division or in interphase (Figure 1A). At the period of anthesis, some cells will no longer divide, but they will protrude slightly above the epidermis surface. These differentiating cells are the fiber initials. Numerous workers have observed fiber initiation the day before anthesis, especially at the crest and at the chalazal end (Aiyangar, 1951; Ramchandani *et al.*, 1966; Joshi *et al.*, 1967; Ramsey and Berlin, 1976a); thus, initiation is clearly not induced by the pollination-fertilization process. Fiber initiation is a part of the total flower opening mechanism, which starts one or two days before anthesis with the expansion of the petals and the elongation of the style and anthers, and which culminates in increased growth of the ovary at the day of anthesis.

Study of the ultrastructure of the outer epidermal layer in *Gossypium hirsutum* by Ramsey and Berlin (1976a) at the day before anthesis revealed some significant changes: at 24 hours preanthesis, all the cuboidal cells had numerous vacuoles containing an electron dense material which was assumed to be phenolic substances. Different cytological changes connected with fiber initiation appears simultaneously in some cells at 16 hours preanthesis, together with the release of the phenolic substances from the vacuoles and an apparent increase in cytoplasm density. Since phenolic substances are known to interfere strongly with IAA-oxidase (Leopold and Kriedeman, 1975; Kefeli and Kutacek, 1977), it is suggested that o-diphenolic compounds are indirectly involved in the original stimulation of the fiber expansion by inhibition of IAA-oxidase with a resulting accumulation of IAA.

However, the metabolic background of the first stages of fiber differentiation may be somewhat more complicated since increase of o-diphenol oxidase activity has also been detected during the same period (Naithani *et al.*, 1981). It may be that different balances between o-diphenols and other phenols in the different

epidermal cells are responsible for the distinction between fiber initials and the remaining epidermal cells.

Fiber initiation appears first at the chalazal part of the ovule and continues progressively towards the micropyle where the first fiber initials are observed at least 24 to 48 hours after anthesis (Joshi *et al.*, 1967; Sheffield, 1936). Meanwhile, and especially during the day of anthesis, a great number of cells continue to divide with an increasing rate in the observed number of mitotic figures. At 1 day postanthesis (DPA) further mitosis occurs but at a gradually decreasing rate. Nevertheless, mitosis has been observed till 10 days after anthesis (10 DPA) in *G. hirsutum* cultivars and till 11 DPA in *G. barbadense* cultivars (Kechagia-Michailidou, 1977).

According to all the reported observations, it is at the day of anthesis that the majority of the lint fibers is clearly initiated.

The fiber initial will first extend above the surrounding epidermal cells and assume a "ballooning" shape. Spectacular changes occur in these cells: the central vacuole moves towards the "ballooning" part and expands further, occupying at 2 DPA almost the complete cell body, including the basal part, leaving only a thin cytoplasmic layer, except at the tip. At that time, only small amounts of electron dense material remain in the vacuole. The nucleus moves towards the tip and increases considerably in size. The original small nucleoli, typical of interphase epidermal cells, fuse together, thus producing a large spherical nucleolus which occupies a major part of the nucleus (Stewart, 1972; Ramsey and Berlin, 1976b) (Figure 1 Bc and C).

FIBER ELONGATION

MORPHOGENETIC ASPECTS

The majority of the morphogenetic processes reported hereafter are based on observation of *G. hirsutum* material. The timing of these processes may differ from one species to another and perhaps slightly among the cultivars of a same species.

Longitudinal expansion, in other words, fiber elongation, already dominates at 1 DPA (Figure 1 Cb), but lateral expansion continues slowly and gives approximately the final diameter to the future fiber at about 4 DPA.

At 1-2 DPA, the hitherto rather blunted fiber tip begins to taper (Figure 1 Cb). Tapering on mature fibers will be abrupt in *G. hirsutum* and gradual in *G. barbadense*.

Orientation of almost all the fiber tips towards the microplylar end of the ovule starts from 1 DPA on and was nicely demonstrated with S.E.M. by Stewart (1975). This may be an expression of polarity along the longitudinal axis of the ovule that perhaps is linked with hormonal influences. The resulting orientation is irreversible and mature fibers will generally form a sharp angle with the seed surface.

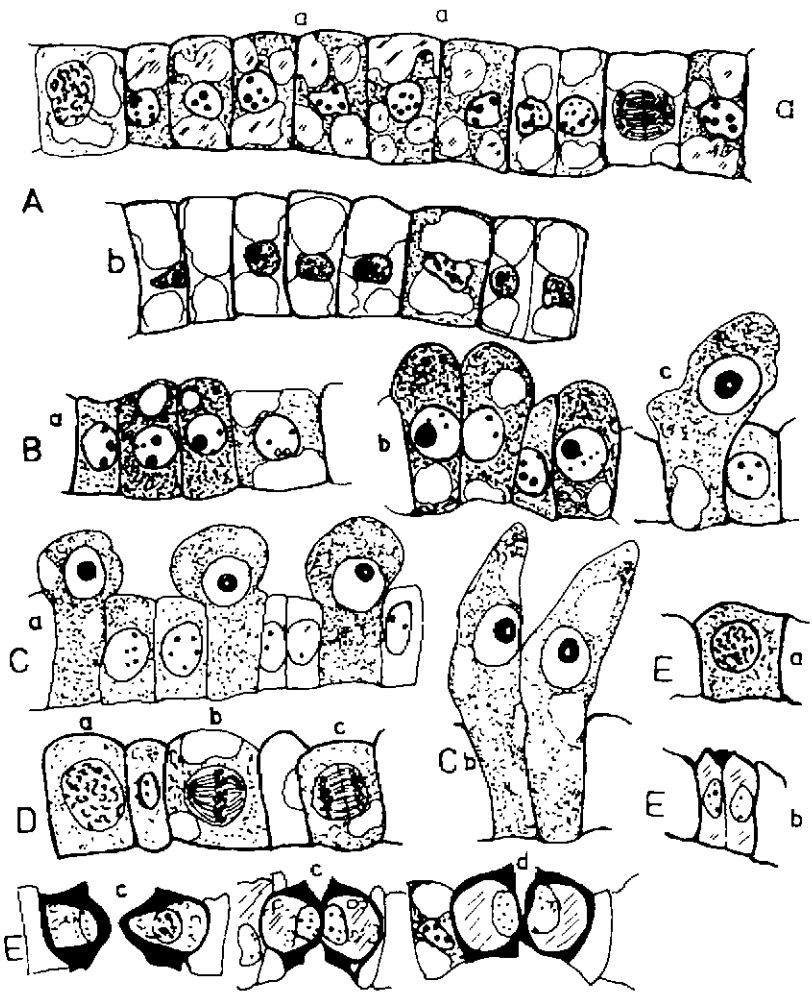

Figure 1. Outer epidermal layer of the cotton ovule during the period of lint fiber initiation.

A. Epidermal layer of cotton ovule one day before anthesis. a, fiber primordial cells; b, cells which will divide the next day, red staining nucleus.

B. Fiber initiation. a, dark type cells, beginning of initiation; b, initials four and c, 28 hours after anthesis (*G. hirsutum)*

C. Fiber initials of *G. barbadense*. a, four and b, 28 hours after anthesis.

D. Mitotic figures. a, prophase; b, metaphase; c, late anaphase.

E. Stoma formation. a, mother cell; b, daughter stoma cells; c, stomata of *G. barbadense;* d, stoma of *G. hirsutum* (after Kechagia, 1977)

Also during this early period, the fibers will form small clusters, their tapering tips adhering to each other, with a certain contortion of the rapidly elongating fibers as a result. This is indeed clearly shown on S.E.M. prints made by Stewart (1975). This contortion generates a spiral configuration of the fiber "tube", and this configuration may have important consequences with respect to protoplasmic streaming and cell wall building.

At about 14 DPA, a typical *G. hirsutum* fiber is already more than 20 mm long and about 20 μm wide; this means a more than 2000-fold volume increase. The thin primary wall and the no less thin cytoplasmic layer enclose a gigantic vacuole. From the very first days after anthesis on, the large nucleus will remain midway between base and tip, which after all seems to be the best position for control of the total fiber activity.

Such enormous and almost uni-dimensional cell growth can only be explained by the combination of at least three exceptional conditions: a considerable metabolic activity, the fast and constant uptake of large amounts of the substance needed for this activity, and the constant formation of a continuously extending and strong primary wall.

ULTRASTRUCTURAL ASPECTS

Many indications of a very high metabolic activity were revealed by electron microscope studies of the fiber cells during the elongation period (Ramsey and Berlin, 1976b; Westafer and Brown, 1976). The cytoplasm contains many lipid bodies, small vacuoles, plastids, mitochondria, single ribosomes, free polysomes, endoplasmic reticulum and dictyosomes with electron dense mature-face cisternae. These dictyosomes are numerous and appear along the entire length of the cytoplasm layer during the elongation phase. Other ultrastructural details can be found in Chapter 26.

Similarities in the nature of membranes are apparent between dictyosome-associated vesicles and plasma membrane-associated vesicles. Many dictyosome vesicles contain "fibrils" morphologically similar to "fibrils" found in the plasma membrane-associated vesicles and in the primary wall, suggesting that dictyosomes are active in both primary cell-wall and plasmamembrane formation. The endoplasmic reticulum is involved in the formation of the central vacuole.

THE NUCLEOLUS: A DRIVING FORCE

As discussed by Kosmidou (Chapter 25), the size of the spherical nucleolus of elongating fibers increases exponentially during the first days postanthesis to a maximum diameter of some 8-10 μm. This maximum size is maintained for several days then decreases gradually, but nucleolus diameters of more than 2 μm can still be observed at 30-40 DPA. In the same chapter the role of phytohormones in fiber development is discussed: gibberellic acid (GA) in combination with auxin exerts a powerful growth stimulation during the very first days after

anthesis, while a constant presence of auxin in the absence of GA seems to be needed for continuation of fiber elongation, and perhaps for secondary wall formation too. Abscisic acid (ABA) can counteract these stimulations, especially during the elongation phase (Dhindsa *et al.*, 1976).

The nucleolus is probably a major site of action of these hormones on fiber development (DeLanghe *et al.*, 1978). Generation of new nucleolar material should be stimulated by GA, but the resulting ribosomal RNA needs to be translocated into the cytoplasm. This output should be stimulated by auxin. Finally, ABA can stimulate output too, but will counteract the GA-action.

Differentiation of the equation for daily fiber growth gives a curve for the rate of fiber growth as a function of days postanthesis. The shape of this curve is rather similar to the shape of the curve expressing nucleolar diameter as a function of days post anthesis (Figure 2). Two main differences between these curves appear: the maximum fiber growth rate is generally reached a few days later than the maximum nucleolus diameter, and fiber growth rate is almost zero at 30 DPA while the nucleolus, although small, still exists at 40-50 DPA.

The link between nucleolus activity and fiber growth can be understood as

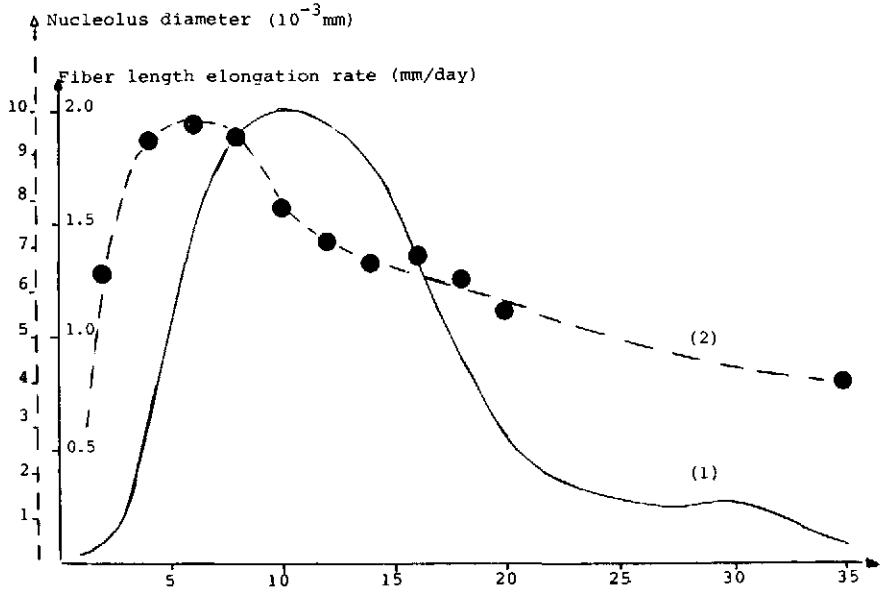

Figure 2. Changes in nucleolus diameter and in fiber elongation rate on the chalazal end of ovules of *Gossypium hirsutum*, cv. 4S.
(1) Mean fiber elongation rate in mm per day (after Michaelidis, 1978)
(2) Mean nucleolus diameter in 10^{-3}mm.

follows: fiber growth rate is almost the direct expression of the total metabolic activity of the expanding cell. The metabolic activity is not only a function of enzymatic activity and of substance availability but in the present case is probably much more dependent on the quality of available enzymes. The quantity of enzymes produced per unit of time is obviously a function of the quantity of active ribosomes (polysomes), and this quantity depends on the nucleolus activity. Given the sequence "nucleolus-ribosomes-enzymes x substrate-expansion", the fiber growth rate should indeed follow in time the change in nucleolus activity. The remaining nucleolus activity between 30 and 50 DPA should be necessary for secondary wall formation, another expression of the metabolic activity.

When the size of the nucleolus as a function of days postanthesis is differentiated, the resulting curve expresses the rate of change in the size of the nucleolus and shows a sharp peak during the first 48 hours after anthesis. This is exactly the brief period when gibberellic acid (GA) exerts the observed strong stimulation of total fiber growth. It is indeed very tempting to locate the site of action of GA in the nucleolus.

The precise mechanism by which the hormones are functioning in the nucleolus needs specialized fundamental research. Although the action of phytohormones on other cellular parts such as plasma-membranes is certainly not precluded here, the amount of work done in this area is considerable, and the results are still rather meager and contradictory. It would perhaps be worthwhile to look for a location of hormonal action in and around the nucleolus.

THE SUBSTRATE SUPPLY

Since the primary walls of elongating fibers are apparently not in direct contact with a vascular system or with a "nutrient" medium, the amounts of substrate needed for the impressive metabolic activity must be supplied by the vacuole. It is, however, not clearly understood how substrate uptake can keep pace with such a rapidly growing vacuole.

The base of the fiber, where this uptake is supposed to occur, does have a special shape. During the early elongation phase, this base is transformed into a "shank" deeply anchored in the epidermal layer, with a "foot" spreading out broadly beneath the surrounding cells of the outer integument. (Fryxell, 1963, 1964). In later stages the secondary wall deposition will extend into this foot, leading to the impression that the cell does not need further contact with the ovule for the final development.

During the elongation period, turgor pressure should obviously play an important role. Potassium malate, partly coming from dark CO_2-fixation reactions, was found largely responsible for this turgor in cotton fibers (Dhindsa *et al.*, 1975). Increase in the activity of the involved enzymes (phosphoenolpyruvate carboxylase, a malate dehydrogenase and glutamic oxaloacetic transaminase) was due entirely to GA_3 when unfertilized ovules of the day of anthesis were cultivated *in vitro*. Abscisic acid (ABA) counteracted these GA_3 effects (Dhindsa, 1978b).

Cotton fiber cells maintain very high turgor during the whole period of their expansion, yet, gibberellic acid is effective only during the first days. This seems to exclude a direct activation of the forementioned enzymes and points to the possibility of a more basic action, perhaps again on the level of nucleolar activity.

THE PRIMARY WALL AND ITS EXTENSION

Transverse sections of elongating fibers show primary walls which remain consistently less than half a micron in thickness. In many cultivars the cells have a cylindrical shape with an almost constant perimeter along more than 80 percent of the length. Tip-growth would permit rigidification of the "older" lower parts of the cell, but it is now evident that, like most other plant cells, the primary wall appears to be desposited evenly and simultaneously on the entire fiber surface (O'Kelly, 1953; O'Kelly and Carr, 1953; Maclachlan, 1977; Ryser, 1977).

CHEMICAL COMPOSITION

In the pectic fraction, protein, glucose and uronic acid are predominant. The hemicellulose fractions contain glucose, uronic acids (fraction 1), galacturonic acid, glucose, arabinose, galactose and rhamnose (fraction 2). Finally, the α-cellulose fraction contains glucose, xylose, galactose and rhamnose (Huwyler *et al.*, 1979).

The relative importance of these constituents changes during elongation. The amount of hemicelluloses increases many times and reaches a maximum in absolute weight at the end of the elongation period. While the absolute content in protein of the primary wall increases during elongation, especially in the hemicellulose fractions (Huwyler *et al.*, 1979), the percentage of nitrogen in the cellulose fraction decreases from 0.5% at about 4 DPA to 0.1% at 21 DPA (Nowak-Ossorio *et al.*, 1976). The most interesting change found by Meinert and Delmer (1977) was the large increase in non-cellulosic glucose, which seemed to be a 3-linked glucan, just prior to the onset of secondary wall deposition. According to them, a sharp decline occurs in protein and uronic acid content at the time of the onset of secondary wall, which, as will be seen later, starts well before the end of elongation.

THE MICROFIBRIL

The basic structural unit of the wall is the microfibril. Some confusion exists in terminology since names such as cellulose fiber, elementary fibril, microfibril, fibril, are applied for the same or for different objects. Bundles of microfibrils, shown electron-microscopically in degraded cotton walls, correspond to the "fibrils" seen in optical microscopy (Kinsinger and Hock, 1948; Willison and Brown, 1977). An extracted primary wall, obtained by elimination of non-cellulosic material, shows the typical woven network of these microfibrils and microfi-

bril bundles. The interwoven pattern makes the length of the individual microfibrils of the cotton wall difficult to evaluate. Most reports agree that the microfibril should be 10-30 nm wide, 5-10 nm thick and several microns long, but some authors still consider such a microfibril as an aggregate of elementary fibrils (called cellulose fibers by Albersheim, 1975), which should be only 3.5 nm wide (Rollins, 1968b).

On the inner side of the primary wall, next to the plasmalemma, the microfibrils are oriented nearly transversely to the cell axis in two more or less opposed directions, while they lay parallel to the axis on the outer side. Both the size and the number of microfibrils increase with the age of the primary wall. These fibrillar dimensions and orientations are considered to be common in the primary walls of the growing cells in most plants. Albersheim (1975) developed the well-known model of primary wall structure from fundamental studies on walls of sycamore cells grown in suspension culture. According to his model cellulose fibers (elementary fibrils) are composed of 40 straight cellulose chains and are linked to parallel chains of rhamnogalacturonan by bridges of xyloglucans and arabinoglucans. While the general application of this model to all primary walls of dicotyledons is uncertain, the fact that galactose and xylose are resistant to even careful isolation from the cellulose of the cotton fibers (Nowak-Ossorio *et al.*, 1976) supports a comparable situation.

PRIMARY WALL EXTENSION

The mechanism of primary wall extension can be understood by combining the Albersheim model with the so-called "multinet-theory" of Roelofsen (1959), according to which the microfibrils move outwards across the primary wall from inside to outside, changing meanwhile their orientation from nearly transverse to parallel with the axis. This occurs in successive lamellae, following the synthesis of new microfibrils. Albersheim suggested that, as the microfibrils slide past one another, covalent bonds in the crosslinking polysaccharides are repeatedly broken and new bonds formed in order to maintain the strength of the wall. This system depends also on the systematic insertion of newly synthesized polymers (Albersheim, 1975; Albersheim *et al.*, 1977). In such conditions and since the outer microfibrils are parallel with the axis, no lateral extension should be possible once the outward microfibril movement acquires the final orientation: the fiber will keep its perimeter and tubular shape throughout elongation. This critical shape-forming period may occur at 1 DPA when longitudinal growth starts to dominate the lateral expansion, perhaps due to the forementioned polarity of the fiber tips towards the micropyle. According to Willison and Brown (1977), the more recent theories for wall growth, proposed by Boyd and Foster (1975) or Roland *et al.* (1975), are not suitable for cotton fiber walls.

The rate of primary wall extension appears thus to be based on two parameters: the rate of synthesis of new microfibrils and related polysaccharides and the rate of reciprocal microfibril movement. The cellular framework for such continual

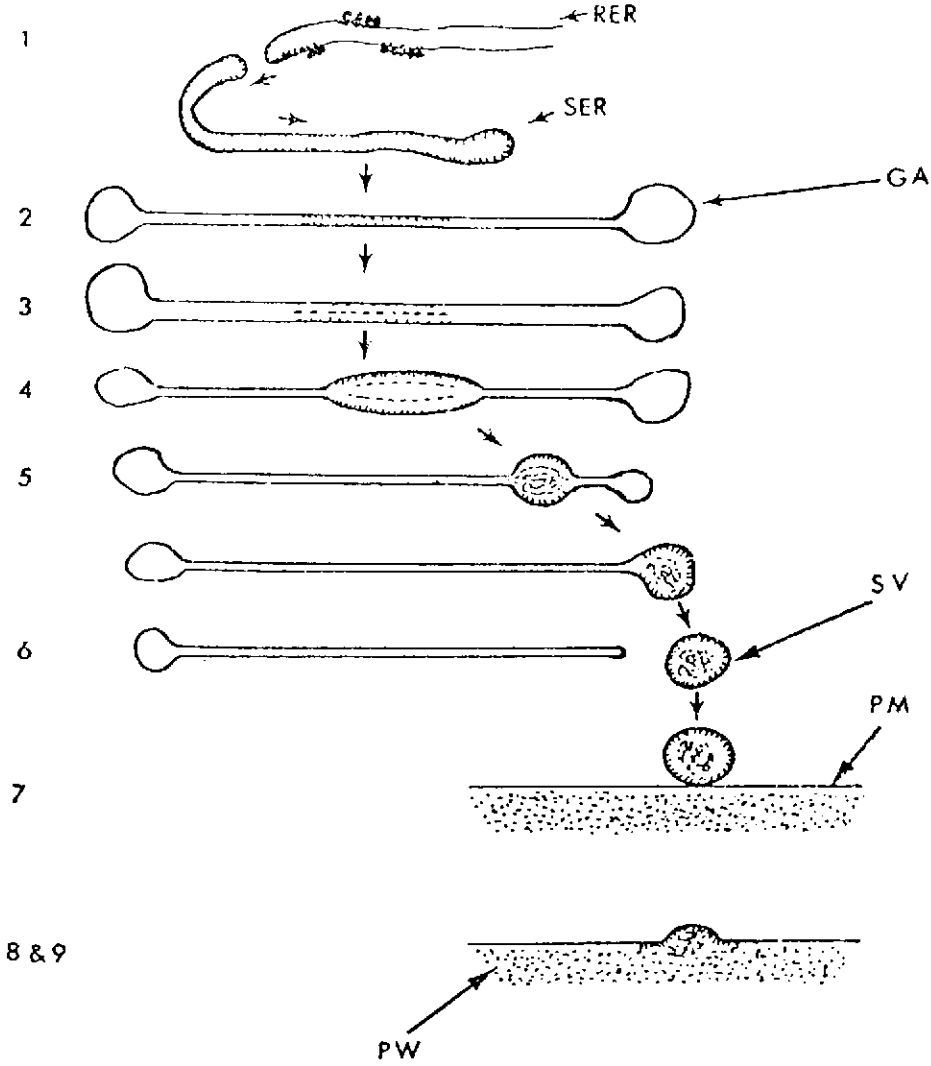

Figure 3. Cross-sectional model of primary wall synthesis in the cotton fibre. The different steps of the primary wall synthesis are explained in the text under the item "Primary wall extension" (after Westafer and Brown, 1976).

synthesis and assembly of the primary wall components is partly a matter of speculation, although great progress was made during the last decade in the study of this process, and ingenious techniques were used in the analysis of various cell

walls. New cellulose is inserted into the inner surface of the cell wall at multiple sites (loci) during growth. From the Albersheim model, one can deduce that both microfibrils and the linking polysaccharides should be synthesized simultaneously since the xyloglucan forms an integral part of the microfibril and since rhamnogalacturonan is a long chain, parallel to the 40 cellulose chains (elementary fibers). Consequently, microfibrils and the associated polysaccharides seem to be constructed at one end of their complex and elongate by tip growth.

R. Malcolm Brown, Jr. and co-workers (Westafer and Brown, 1976; Willison and Brown, 1977) propose the following attractive schemes for primary wall building and extension in the growing cotton fiber cell (Figure 3):

> "Synthetases for matrix substances and, perhaps, for cellulose are made in the endoplasmic reticulum. (1) These enzymes are transferred to the Golgi apparatus via membrane flow and are incorporated within the inner surfaces of the cisternal membranes. (2) Substrates in the cisternae of the Golgi apparatus react with enzymes bound to the cisternal membranes, forming incipient secretory products. (3) The products are released from the inner surfaces of the cisternal membrane into a central dilatation. (4) The dilatation moves laterally, transporting the products and membrane to the periphery of the cisterna forming a nascent secretory vesicle. (5) The secretory vesicle separates from the cisterna and migrates to the plasma membrane. (6) The membranes of the secretory vesicles and the plasma membrane fuse and the product is released via exocytosis. (7) The products are incorporated into the growing primary cell wall; and enzymes (perhaps including cellulose synthetases) transported within the secretory vesicle become exposed to the cell exterior where they initiate synthesis while: a) attached to the membrane, or b) existing free in the periplasm, or c) attached to components of the cell wall itself." Plasmamembrane bounded microfibril synthesizing centers move in the plane of the plasma membrane, spinning out microfibrils as they go. These microfibril synthesizing centers move along a slow helical path towards either end of the fiber such that thin lamellae consisting of uninterrupted microfibrils are produced. The helices of these lamellae are alternatively left-handed and right-handed. Extension of the fiber tends to increase the pitch of the helices, giving rise to the netlike patterns described in multi-net-growth." (Westafer and Brown, 1976)

Fiber elongation presupposes, apart from the high extensibility of the primary wall, a considerable increase of the surface of the various membranes. The observations of Ramsey and Berlin (1976b) and Westafer and Brown (1976) clearly show that the numerous dictyosomes of the Golgi apparatus continually supply new membrane both to the plasmalemma and to the tonoplast by intercalary addition.

Finally, given the constant strength of the primary wall, the microfibrils need to be reconnected repeatedly during their movement (Albersheim, 1975). Albersheim proposes that auxin-induced expansion promotes the cleavage of the arabinan-galactan and that growth may involve the insertion of new wall material into the cleaved cross-connecting arabinan-galactan (Albersheim *et al.*, 1977). But, there is still no clear evidence for the mechanism by which the cleavage and recombination proceeds. He speculated that an enzyme in the wall mediates the transfer of bonds between polysaccharides, and that it could promote growth specifically. As yet, no such enzyme has been identified, and until it is found, "we will remain in the dark as to the exact nature of cell wall-loosening" (Cleland, 1977).

THE OVERLAPPING PHASE

SIMULTANEOUS ELONGATION AND WALL THICKENING

Early observers (Balls, 1915; Anderson and Kerr, 1938; Rollins, 1968a,b) stated that secondary wall thickening starts after the cessation of elongation. Evidence is now accumulating for the fact that secondary wall thickening begins before the completion of fiber elongation (Benedict *et al.*, 1973; Schubert *et al.*, 1973; Kohel *et al.*, 1974a; Meinert and Delmer, 1977). Since the observations were based on mean data, such as substantial increase in dry lint weight per seed during further increase of halo length, one could argue that the evidence does not necessarily mean that the overlapping occurs in individual fibers. Indeed, one can suppose that an increasing number of fibers stop elongation and start wall thickening while a decreasing number continue elongation with only a primary wall. But, Schubert *et al.* (1976) found in *G. barbadense*, cv. "Pima S-4", that by the time elongation ceased, almost 90% of the final lint dry weight per seed had been reached. Moreover, in a careful study of lint elongation on cultivars of *G. hirsutum* and *G. barbadense*, the surface of the seed was subdivided into 9 regions, and lint length measured during the entire elongation period (Michaelidis, 1977). This study clearly showed that elongation rate was strictly synchronous on the whole seed, despite the different lengths per region, and that elongation ceased for all seed regions at about the same day postanthesis.

The deduction from the combination of these results is evident: overlapping of elongation and secondary wall formation occurs at the level of the individual fiber. This conclusion is of fundamental importance for a better understanding of the two processes, the production and extension of the primary wall and the building of the secondary wall, which apparently occur simultaneously during a large time span.

GRADUAL AND ABRUPT CHANGES IN WALL COMPOSITION

In her study of the degree of polymerization (DP) in cotton fiber walls, Marx-Figini (1966a) found that the DP starts to increase at about 15 DPA, reaching a

plateau of DP 1400 just before 20 DPA. Cellulose biosynthesis increased around 10 DPA and became important at about 16 DPA. It is, however, hazardous to assemble indications of early secondary wall activity from various literature sources since different laboratories worked with different cultivars or even species. Environment too has a definite influence on the rate of elongation and of wall thickening.

Overlapping of elongation and thickening could mean gradual changes in the related metabolism and a gradual increase in cellulose, for instance. But Meinert and Delmer (1977) found rather abrupt changes in the rate of cellulose increase with a first peak at about 16 DPA followed by a decrease for 2 days and then a sustained increase culminating at about 27 DPA. The synchrony of lint elongation (Michaelidis, 1977) and the fact that fuzz fibers probably do not begin secondary wall deposition before the true fibers (Beasley, personal communication), seem to exclude influence of heterogeneity in the material used for cellulose analysis. Moreover, the decrease in elongation rate was less at about 15-16 DPA in cultivars of two *Gossypium* species (Michaelidis, 1977). Glucan synthetase activity shows a sharp peak between 15 and 19 DPA (Delmer *et al.*, 1977) and, as will be explained further, its first product is most probably not cellulose but β-1, 3-glucan which may be an intermediate in the synthesis of cellulose. A study of environmental influences also gave results that fit best with the concept of fundamentally different factors controlling elongation versus secondary wall deposition (Gipson and Joham, 1968b).

Given the different indications, it seems better to abandon the idea of "smooth transition" between elongation and thickening and to accept that a new process is starting rather abruptly during the elongation period. The fiber forms an integral part of a complex assembly: the seed. The fuzz and the non-fiber epidermal cells also start secondary wall formation at 16-19 DPA (Beasley, personal communication; Berlin, 1979). At about the same period, the embryo begins to expand rapidly, soon followed by a spectacular weight increase (Ihle and Dure, 1970). Thus, the entire seed shows a change in metabolism, resulting among other things in the onset of secondary wall deposition in the lint fibers. (See Chapter 20 for more detail on related events during development of the boll). A causal relationship, in the sense that this onset of secondary wall deposition should progressively inhibit further elongation (Meinert and Delmer, 1977) is possible but not evident (Schubert *et al.*, 1976). The acceleration of the elongation rate stops at about 5 DPA. The rate is constant until about 12 DPA, then decreases thereafter (Michaelidis, 1977). No other parameter is in fact needed in order to explain the "phasing out" of elongation.

THE S_1-LAYER

The first layer of the secondary wall is distinct from the subsequent ones in many aspects: the terms "winding layer" (Hock *et al.*, 1941) or "S_1-layer" are frequently used for it (Figure 4). It is said to serve as a transition layer between

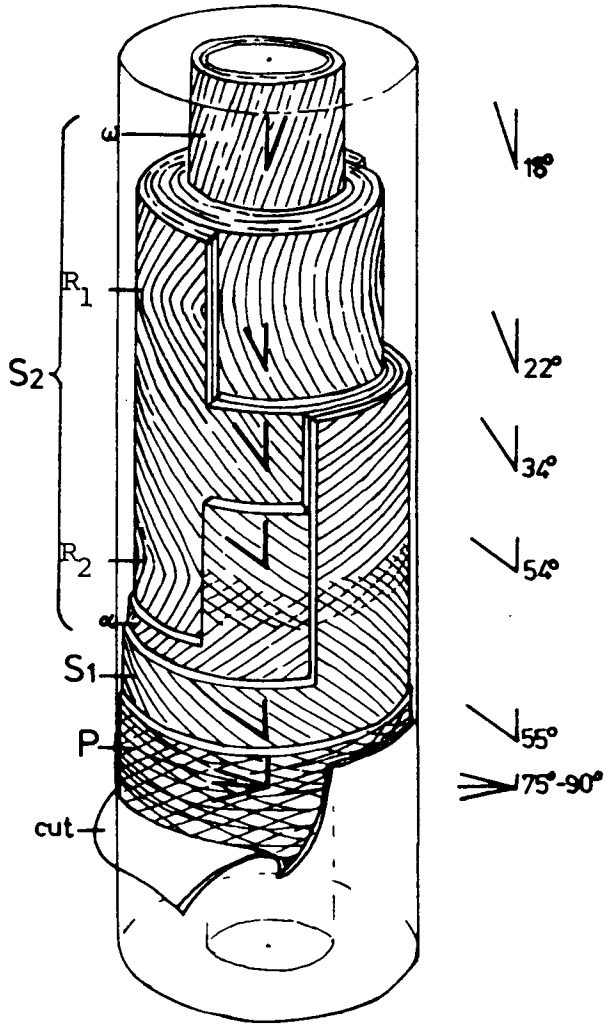

Figure 4. Schema of a mature lint fiber.
Cut = cuticula
P = Primary wall
S_1 = S_1-layer
S_2 = secondary wall, layers $S_{2\alpha}$ to $S_{2\omega}$
R_1 = reversal with bended fibrils.
R_2 = reversal with fibrils "crossing" or meeting on opposed fibril angle.
55° = fibril angle
(after Waterkyn, 1974)

the network of the primary wall and the oriented fibrils of the following layers, called S_2-layers (Rollins, 1968b). The fibril angle is generally wider than in the S_2-layers, but much smaller than the angle of the primary wall microfibrils. Most striking however is the fact that the fibril helix of the S_1-layer is opposite to that of all the following S_2-layers. Observation of the S_1-layer is difficult and normally requires a swelling treatment by cuprammonium hydroxide (Cuoxam). If fibers are oxidized first with "4% $KMnO_4$ + H_2SO_4 droplets" and then swollen with Cuoxam, the primary wall and the cuticle separate in helicoidal bands. The underlying S_1-layer determines the S or Z orientation of these bonds and their helical angle with respect to the fiber axis (Waterkeyn, 1974). With NO_2-oxidation, the primary wall and S_1-layer split into fine fibrils or into broad spiral bands (Rollins, 1945). In fibers swollen with Cuoxam, the primary wall and the S_1 layer both play a part in restricting uniform swelling of the wall (Kerr, 1946). All this could indicate that S_1-deposition is more related to the primary wall than to the true secondary wall (Rollins, 1945). The S_1 layer could be detected as early as 10 DPA on unswollen fibers and was made up of a system of bands or tapes lying at "an angle" to the axis of the fiber (Rollins, 1968a). So long as secondary wall deposition was considered to occur only after cessation of the elongation, such early presence of S_1-traces was confusing. Willison and Brown (1977) suggest that the S_1 layer may simply represent that part of the secondary wall which has undergone extension. But cross sections of fibers at 19 DPA show considerable secondary wall (Schubert *et al.*, 1973). Since 40-50 percent of the final dry weight can be reached by the end of the elongation period (between 25 and 30 DPA), much more than the S_1 layer must have been deposited. Moreover, the helix-orientation of S_1 has consistently been found to be opposed to that of the so-called S_2-layers, but not necessarily on all parts (Kerr, 1946). The difficulty of understanding the S_1-layer phenomenon is obviously connected to the compromise between the production of a still extending primary wall and that of a secondary wall which tends to be rigid.

THE SECONDARY WALL

PHYSICAL COMPOSITION

Cross sections of mature fibers, swollen with e.g. cupramonium hydroxide, show a series of concentric layers, the number of which correspond roughly with the duration in days of secondary wall formation. They were called "daily growth rings" (Balls, 1919).

Kerr (1937a) proposed that these rings consist in fact of two layers: a compact one associated with a warm growth-period during daylight, and a more porous one formed during cool night hours. Indeed, with decreasing contrast in temperature between day and night, the rings become less apparent or even disappear (Berriman and Benedict, 1963). Grant *et al.* (1966) showed that fibers grown under constant temperature conditions are ringless, regardless the light, and that only

the fluctuations in temperature are responsible for rings. The interest in this temperature controlled layering increased with the suggestion of Dupre (1959) that elongation of the fibers under high load, as well as reversibility of such extension, are made possible by the slipping of the layers.

Grant and co-workers (Grant *et al.*, 1966, 1970, 1972) proved however, that absence of rings does not lead to major changes in physical properties. The team considers "growth rings" as artifacts, since the rings are revealed only after treatment with cupriethylene diamine or with cuprammonium hydroxide. These are solvents of cellulose, so they suggested that the rings are a result of differences in the dissolution rates of cellulose deposited at low versus high temperatures.

However, even in ringless fibers, a fundamental layering appeared indirectly as sheets of lamellae when walls were fractured after various manipulations (Tripp *et al.*, 1951; Isings, 1964). According to Grant *et al.* (1970) the associated preferred plane of shear could be the real regions for "internal movement in the cotton fiber with the helical fibril arrangement". Polymerization of methacrylate in fiber cell walls results in expansion, and a pattern of concentric layers 35 nm thick is seen. Grant *et al.* (1972) suggested that these are the basic layers.

Construction of microfibril bundles is much more important in the secondary wall than in the primary wall. The bundles with microfibrils still fasciated (Willison and Brown, 1977) run parallel at an angle to the axis that decreases from the outside to the inside (Waterkeyn, 1974). Willison and Brown (1977) observed an undulation of the bundles with comparable wavelength in both the primary and secondary walls but with a much reduced amplitude of 20-40 nm in the secondary wall.

Complexes of microfibril bundles appear under the optical microscope as "fibrils" with the typical helicoidal arrangement. A unique feature of cotton fiber cells is the intermittent change in the direction of the twist of the helix. These "points" are called "reversals". At most reversals the orientation of the fibrils changes abruptly toward an opposed direction, with each fibril apparently bending along an arc (Figure 4 R_1). At other reversals, two helices of opposed directions encounter at the section-plane and fibril ends seem to overlap (Figure 4 R_2) (Anderson and Kerr, 1938).

CHEMICAL COMPOSITION

Data on the chemical composition of cotton fiber walls are based on the analysis of entire walls, primary wall included. But, the comparison of the composition of maturing fibers with that of elongating ones leads to the conclusion that hemicelluloses and pectic substances must be very rare in the secondary wall. The fact that an arabinogalactan was isolated from fibers at the stage of intensive secondary wall formation (Buchala and Meier, 1981) should not be misunderstood. As the authors noted, even in that stage the hemicellulose is located either in the primary wall or in the cytoplasm. An important decrease was found in the absolute amounts of hemicelluloses in the fiber walls during the period of secon-

dary wall thickening (Huwyler *et al.*, 1979). This fact seems to exclude any presence of hemicelluloses in the secondary wall.

Marx-Figini (1966b) found that the degree of polymerization of the cellulose throughout the period of secondary wall building was constant and much higher (14,000) than the DP of primary wall cellulose (1000-3000). In *G. herbaceum* crystallinity of the cellulose appears at 20 DPA, increases rapidly and remains constant from 25 DPA on. (Nowak-Ossorio *et al.*, 1976).

Large differences in crystallinity should not mean that celluloses of the primary versus secondary wall are different. In both cases, the celluloses may consist of native cellulose I crystals, but in the primary wall these crystals will have a poor lateral organization of the network of inter-chain hydrogen bonds (Chanzy *et al.*, 1978).

THE PROCESS OF SECONDARY WALL FORMATION

The considerations about physical and chemical composition point to the high probability that the difference between primary and secondary wall construction is the result of two basically different cellulose assemblage systems. Willison and Brown (1977) detected granules of 20-30 nm diameter bound to the outside of the plasmalemma of maturing lint fibers which they considered as comparable to the globules associated with the ends of microfibrils in corn roots (Mueller *et al.*, 1976). They suggested that groups of microfibrils are synthesized close together spatially and temporally. The globules on the outside of the plasmalemma may be enzymic complexes concerned with this synthesis and assembly of the cellulose microfibrils (Willison and Brown, 1977).

As they move across the cell surface, they would add new glucan to microfibril ends (Willison, 1978). The constant DP, together with the fact that cellulose fractions of the secondary wall contain a constant amount of a protein which cannot be removed by available isolation techniques, led Nowak-Ossorio *et al.* (1976) to the conclusion that each cellulose chain is firmly attached with its synthesis apparatus. This deduction was supported by the results of Huwyler *et al.* (1979). If this is so, microfibril bundles of secondary walls are increasing in length by tip growth, and glucose residues are added to them simultaneously at all the cellulose chains they contain.

In an attempt to explain the changes in fiber strength at or between the reversals, Raes *et al.* (1968) proposed a model for the origin of the reversal. They postulated that during elongation, a number of "growth sensitive annular rings" appear at irregular distances along the fiber axis. Cellulose would be synthesized either on both sides of such rings with opposite helical deposition of fibrils and "curved fibril-reversals" at the site of the ring, or on one side only (towards base or tip of fiber) with a sequence of helices in the same or opposed directions and "over-lap-reversals" in the areas where the growing "zones" would meet. The Raes-model fits well with the strength behaviour of individual fibers, and its adaptation to include recent findings about cellulose synthesizing sites is possible.

The annular rings should be "synthesizing zones" which should actually move along the cell surface in the proposed directions. The genesis of the rings should occur during the second period of elongation when secondary wall formation starts (see Overlapping Phase). However, a number of questions subsist, irrespective of the present precarious position of the "mobile synthesizing zone". For example, why is orientation of the helix of the S_1-layer opposed to that of the rest of the secondary wall, and why does the helix angle decrease from out-to inside throughout the secondary wall?

THE CYTOPLASM

Important changes in the cytoplasm occur during the period of secondary wall formation (Berlin, 1970; Ramsey and Berlin, 1976b; Westafer and Brown, 1976). At 30 DPA, very little cytoplasm is recognizable, dictyosomes have almost disappeared and the numerous unattached ribosomes seen during the elongation phase are replaced by endoplasmic reticulum (ER) associated ribosomes in a spiral polysomal configuration. There are indications that ER membranes acquire characteristics which may permit fusion with the plasmalemma. Microtubules, which are rarely observed during the elongation period become numerous during secondary wall thickening. They look "attached" to the plasmalemma and are oriented parallel to the microfibrils. That microtubules should control the orientation of cellulose deposition is still a matter of controversy (Preston and Goodman, 1968; Newcomb, 1969; Chafe and Wardrop, 1970; Robards and Kidwai, 1972; Picket-Heaps, 1974; Sterling, 1975). It has, however, been found that in cotton fibers, the microtubules do parallel the microfibrillar pattern even through the reversals (Yatsu and Jacks, 1981). If this observation is confirmed, then the arrangement of microtubules in the cytoplasm needs careful study. Since the direction of the fibrils in the S_1-layer is opposed to that of all the other fibrils, it would be necessary that a general switch in microtubular orientation occur at a particular "moment" after anthesis.

The hormone ethylene is known to control the direction of cell growth, probably through its effect on microfibril orientation (Richmond *et al.*, 1980). Ethylene treatment has been shown to change the orientation both of microtubules near the plasmalemma and of recently deposited cellulose microfibrils in pea epicotyl cells (Lang *et al.*, 1982). Changes in ethylene content during cotton boll development have been demonstrated (Guinn, 1982). Further study on the possible role of ethylene on microtubule orientation in developing lint cells could be beneficial for a better understanding of microfibril orientation in the secondary wall.

CELLULOSE BIOSYNTHESIS

Although cellulose is one of the most widespread substances in the plant kingdom, its biosynthetic pathway is still not known, despite many attempts to find the precursors and the enzymes involved (Delmer, 1977). The massive secondary wall of cotton fibers with almost pure cellulose is an obvious tool for

such study, and several recent publications have dealt with cellulose synthesis in cotton fibers grown *in vitro* or *in vivo*.

At the onset of secondary wall formation in cotton fibers a sharp rise in noncellulose glucose, together with a substantial increase in cellulose, was clearly observed by Delmer (1976). A "UDP-glucose: glucan synthetase" proved to be highly active in the early secondary wall formation period. Under *in vitro* growth conditions this enzyme produced a glucan with predominantly β-1,3 linkages (Heiniger and Delmer, 1977). The *in vitro* rates of glucan synthesis in the detached fibers during development is within the range of the *in vivo* rate of cellulose synthesis (Delmer, 1976). Huwyler *et al.* (1978) detected large quantities of β-1,3-glucan (callose) in naturally grown 20-40 DPA old fibers. Delmer suggested that a very active turnover from a β-1,3-glucan into cellulose occurs during secondary wall formation, since β-1,3-glucans, such as callose, normally do not have a structural role. But, in a later publication (Maltby *et al.*, 1979) she and her group announced that pulse-chase experiments failed to show any indication of such turnover. With intact cotton fibers, Meier *et al.* (1981), also using the pulse-chase method, did find a high turnover of callose. By means of a specific fluorescence method, Waterkeyn (1981) showed that the callose is always localized in the innermost layer bordering the cell lumen and can be found throughout the entire period of secondary wall thickening. He postulated that most plant cells normally possess a permanent noncellulosic sheet or interface just outside the plasmalemma. In this "matrix" the newly synthesized cellulose chains and/or microfibrils undergo a sort of "maturation" and are oriented before their definitive incorporation in the highly organized cell wall. He suggests also that the amorphous glucan, which is callose, may contribute to the cell wall plasticity, promoting the gliding and passive shifting of the wall microfibrils. Given the overlapping phase when elongation and secondary wall deposition occur simultaneously for many days, "stress situations" seem unavoidable along the entire cell wall, and callose may play a key role as a sort of "lubricating" agent.

The question to what extent callose turnover leads to cellulose synthesis is still open. The (1→3) β-D-glucanases detected by Meier *et al.*, (1981) are not necessarily working as transglucosylases. Indeed, it was demonstrated by Carpita and Delmer (1981) that the rate of synthesis and turnover of UDP-glucose was more than sufficient to account for the combined rates of accumulation of sucrose, steryl glucosides, β-1,3-glucan and cellulose. In other words, there would be no need for transformation of callose into cellulose. On the other hand, one should not overlook the fact that the so-called "dead fibers", where no trace of a secondary wall is seen, even at the period of boll maturity, contain considerable amounts of callose (Waterkeyn, personal communication).

DEHYDRATION OF THE COTTON FIBER

When mature cotton bolls open, the fibers lose their water content and dry out; the tubular cell becomes a twisted ribbon with a kidney-like cross-section. The way fibers have developed may greatly influence the drying pattern. Yet, the dehydration process irreversibly generates many important technological properties of the cotton fiber. For instance, the angle of the many twists, the convolution angle, is negatively correlated with fiber tenacity (Duckett and Goswami, 1979), and the extensibility of normal dry fibers is two to three times less than that of never-dried ones (Berkley and Kerr, 1946). It has even been assumed that most of the crystalline cellulose is formed by dehydration (Colvin, 1972), but never dried fibers are already highly crystalline (Ingram *et al.*, 1974). These last authors found also that the dehydration leads to irreversible hydrogen bonding between the microfibrils, and that this molecular change is responsible for the loss in "slippage" between fibrils, and thus, for loss in extensibility.

A real bilateral structure of these dried fibers was observed by Kassenbeck (1970) after enzymatic degradation. This asymmetry was further examined by Waterkeyn (De Langhe *et al.*, 1979). Dry fibers, treated with alkaline solutions, shorten considerably and "uncollapse". In polarized light such fibers show two opposite helicoidal lines, indicating the demarcation between two alternating helicoidal ribbons. These lines are formed by highly crystalline cellulose fibrils which twist in the same direction as the convolutions and change their direction at the reversals. They were observed on fibers dried as early as 22 DPA (Waterkeyn, 1974). The two ribbons between the lines correspond to the convex (dorsal) and the concave (ventral) side, and drastic action by degrading agents shows that their walls have unequal resistance which is much lower than that of the double helix.

The accessibility of the dried fibers to chemical reagents is, consequently, very unequal and related to the twisting. The key question unanswered is whether the twists are the consequence of an initial heterogeneity created during fiber development, and if so, when exactly and how, or is the heterogeneous structure just the result of mechanical "force-fields" created during the dehydration? Reversals might play a role in the creation of such unequal tensions (Ingram *et al.*, 1974).

COTTON FIBER POPULATIONS

NORMAL DISTRIBUTION OF FIBER LENGTH IN SEED COTTON

Important differences in length exist among the thousands of fibers on a single seed. This variation represents up to 98% of the total variation in the harvest of an inbred cotton line (Richmond and Fulton, 1936). Part of this variation is due to difference among regions of the seed where the mean fiber length decreases from chalazal end towards the micropylar end (Iyengar, 1939, 1941a, 1947; Krishnan and Iyengar, 1960). That other properties such as breaking load, weight, diame-

ter and maturity also vary along the regions of a seed was stressed by Moore (1941) who used the term "fiber population". Similar results were obtained by Iyengar (1941b) for different cotton species.

Variation in fiber length, ranging from less than 1 cm up to more than 6 cm in *G. barbadense* cultivars, is a serious hindrance for yarn and fabric manufacturing (Berkley, 1949). It also complicates the evaluation of characteristics such as maturity and fineness.

Fiber length distributions in samples of bale cotton are almost always asymmetric and negatively skewed in as much as the samples contain a large number of short to very short fibers. Even the usual comb sorter methods for measuring fiber length will give the asymmetric frequency distribution. Yet, the shape of the cumulative frequency curve thus obtained is considered as characteristic for cotton varieties (Christidis and Harrison, 1955).

Length variation was found to be correlated with variations in other properties such as perimeter, maturity, fineness, strength, fibril angle and convolution angle, all of which play a part in the ultimate quality of a yarn (Iyengar, 1939; Petkar *et al.*, 1977; Morlier *et al.*, 1951; Warwicker *et al.*, 1966; Lord, 1961; Hessler, 1961). With an asymmetric frequency distribution, the global expression of a fiber characteristic in terms of mean length, mean maturity, etc. . . . are almost useless. This has led to elaborate methods which attempt to correctly express the total variation in the characteristic under study (Lord, 1961).

In contrast to bale cotton samples Wakeham (1955) found that cotton fibers, as they grow on the cotton seed, are in fact remarkably uniform and that the distribution of fiber length is normal. The fundamental importance of this observation, with respect to the understanding of variation and characterization of cotton fibers, may have been somewhat overlooked. When, from any region of the cotton seed, a group of about 200 fibers is carefully pulled out with tweezers and the length of the fibers measured one by one, a normal frequency distribution of fiber length is observed. This normal distribution has been confirmed during two growth seasons for a number of cultivars representing the 4 cotton species, *G. hirsutum, G. barbadense, G. arboreum* and *G. herbaceum* (De Langhe *et al.*, unpublished results). Variation in fiber elongation appears to occur at random along the whole surface of a cotton seed. Near the micropyle the fibers are indeed much shorter, and coarser too, but the amount of these fibers is minimal, and they are certainly not a cause of significant deviation from normality of the distribution.

The effect of mechanical lint removal processes, including comb sorting, is breakage of an important number of long fibers. This points to the importance of the attachment force of the fiber to the seed (Burkitt, personal communication). Strong attachment should lead to preferential breakage at a weak point along the fiber. About 16 percent of the fibers can break during mechanical removal, and a somewhat higher percentage of the remaining basal parts break again during subsequent removal (Lord, 1963). The difference in asymmetric fiber length

frequency distribution between cotton varieties after mechanical removal is probably a reflection of differences in fiber attachment.

MORPHOGENETIC RELATIONS BETWEEN LINT CHARACTERISTICS

Many attempts have been made to determine if relations exist among the fiber properties with technological importance, such as length, maturity, fineness, tensile strength. Knowledge of these relations would enable technologists to program better any treatment of the cotton before manufacturing yarn and fabric. Breeders and cotton growers, on the other hand, would be able to "translate" the properties in terms of controllable morphological selection criteria. Unfortunately, many contradictionary results came out of these studies. Maturity was found to be either positively (Petkar *et al.*, 1977; Rajaraman and Nanjandayya, 1955; Pillay and Shankaranarayana, 1961) or negatively correlated with fiber length (Fiori *et al.*, 1959; Kechagia-Michailidou, 1977). Analogous situations appeared for other properties, but it was realized that many of them may be the result of different instrumentation or manipulation (Nanjundayya, 1951; Grant and Morlier, 1948; Chytiris, 1961; Calkins, 1961; Iyengar, 1961; Fiori *et al.*, 1961) or sampling (Morlier *et al.*, 1951). Moreover, some relation trends depend on the cotton species (Iyengar, 1939). Some of the contradictions can be explained by the fact that, in some cases, samples from several cultivars were examined (intervarietal relation), while in other cases, the research material contained only fibers of one and the same cultivar (intravarietal-relations). It is well known that the longer fibers of *G. barbadense* do have a smaller perimeter, when compared with fibers of *G. arboreum*. But such a relation obviously cannot automatically be applied to a fiber population from the same cultivar.

A major part of the complication may well be associated with the artificial creation of the asymmetric fiber length distribution. Long fibers develop at the chalazal end of the cotton seed, and they are frequently less mature (Michaelidis, 1977). With mechanical fiber removal, these fibers can break several times and "produce" numerous pseudo-short and less mature fibers. It is easy to see how this artifact can complicate the pattern of maturity, fineness, fabric strength, etc.

Comparison of mean lengths and mean perimeters of fibers from different regions of a seed gave a negative correlation, but different cultivars gave different inclinations for the linear regressions (Michaelidis, 1977; DeLanghe *et al.*, 1979). Such indication of a dimensional relationship of fibers on the level of a seed needs further study in view of its potential importance for the explanation of the other characteristics. On the basis of the regression of fiber length on fiber perimeter, fiber volumes and fiber surfaces can be calculated. With the exception of the small number of short fibers at the micropylar end, variation in fiber volume on a seed surface may be rather small, consequently, fibers with the same volume may develop different wall surface areas and secondary wall thicknesses, depending on the ratio between length and perimeter.

A positive correlation was found by Kechagia-Michailidou (1977) between

fiber perimeter and the perimeter of the fiber initials. Conclusively, a major part of the variations in many fiber properties may be generated through the original variation in the size and growth potential at about the anthesis period of those epidermal cells which differentiate into lint fibers. As for other technologically important characteristics, Duckett and Goswami (1979) for instance, demonstrated that changes in the ratio of fiber perimeter to wall thickness are responsible for deviations from the normally negative correlation between fiber tenacity and the degree of convolution.

LINT PRODUCTION AND LINT QUALITY

ENVIRONMENTAL AND GENETIC STRESSES

Many links between environment or genotype and lint development are perhaps simple and clear, but they are complicated by observations performed on mechanically removed fibers, since this technique leads to the artificial asymmetric frequency distribution of fiber properties. Results dealing with stress influences should, therefore, be considered with caution since they may not reflect biological reality. Thus, much global information about these influences in classical handbooks on cotton is still of current value (Christidis and Harrison, 1955; Elliott *et al.*, 1968).

The rates of fiber elongation and of secondary wall thickening are both influenced by temperature. The optimal temperature for fiber elongation is surprisingly low and very rarely exceeds 25C (O'Kelly and Carr, 1953; Hessler *et al.*, 1959; Morris, 1962; Stockton and Walhood, 1960). Contrary to earlier statements, Gipson and Joham (1969) found that fiber elongation is temperature sensitive during the first days after anthesis and becomes temperature independent after 15 DPA. (See Chapters 5 and 20 for additional discussions and interpretations). Smutzer and Berlin (1979) confirmed in *G. hirsutum* L. var. Dunn 56C that fiber elongation was optimal at 15C, and that fiber initiation under 10C or 25C conditions resulted in shorter elongating cells, less apparent electron dense polyphenolic compounds, retardation of vacuole formation and a lower amount of endoplasmic reticulum. An analogous parabolic trend in temperature influence was found for different varieties by Gipson and Joham (1968). Cultivars with longer fibers were more sensitive for lower temperatures (Gipson and Ray, 1969; but see Stewart, Chapter 20).

A comparable trend exists in the relation between temperature and various properties of the secondary wall but at a higher temperature level. In experiments with constant growth conditions, Grant *et al.* (1966) found the shortest period between flowering and boll opening (41 days) was at 29.5C and with constant light. Fibers grown at 21C had thinner walls, less compact cellulose, lower extensibility and lower crystallinity measured by X-ray angle (Grant *et al.*, 1970).

According to Gipson and Joham (1968) the night temperature should play a key role. Most influences are linked with the rate of cellulose synthesis (Hessler *et*

al., 1948), but contradictions appear. Rapidly developing cottons are likely to be strong (Hessler, 1961), but late plantings in the season on the Texas High Plains, meaning growth under lower temperature conditions, gave shorter but stronger fibers (Bilbro and Ray, 1973). It may be stated with Hessler (1961) that "anything less than optimum fiber development under varying environmental conditions can conceivably result in innumerable types of fiber structure". Since secondary wall development in fibers and in other epidermal cells of the same cotton seed is synchronous (Berlin, 1979), the temperature dependent rate of cellulose synthesis is probably only a part of a more general temperature dependence at the level of the cotton boll. Higher night temperatures shorten the boll maturation period while incomplete boll maturation is due to low minimum night temperatures (Yfoulis and Fasoulas, 1978). But, the phenomenon cannot be explained in simple terms of lower photosynthate availability, since at these lower temperatures an increase in sugars is observed parallel to the decrease in cellulose synthesis (Hessler *et al.*, 1959).

The influence of humidity on fiber development is less well documented. Higher humidity conditions during fiber development result frequently in longer fibers with lower tenacity and higher reversal density, but varietal interaction can be strong (Fransen and Verschraeghe, 1967). The same authors found that irrigation increased significantly the reversal density in the three varieties observed. Buxton *et al.* (1973) found that dry growth conditions led to shorter fibers but had no effect on fineness or strength.

Increase in light intensity from 4000 to 60,000 lux can result in the doubling of the rate of cellulose synthesis (Marx-Figini, 1966b). Such high rates are not necessarily beneficial for wall quality. Rapidly formed walls in 30-35 days old bolls on plants grown under glasshouse conditions showed a lower tensile strength for the same or even greater thickness than more slowly formed ones (DeLanghe *et al.*, 1979).

THE NEED FOR "LINT QUALITY" GENERATING MODELS

For many crops grown all over the world, yield, including resistance to diseases and adverse growing conditions, plays a dominant role in the related agronomic research. For the cotton plant both lint quality and yield are important in the economic evaluation of the product.

Excellent models which simulate plant growth have been elaborated for cotton, and they have been worked out down to the level of lint percentage of the boll weight (Jones *et al.*, 1980; Constable and Rawson, 1980). Current research aims also at improving the morphogenetic aspects in the simulation of cotton plant growth (Mutsaers, 1982; See also Chapter 19).

McArthur *et al.* (1976) advised that future research should be oriented towards improving the subsystems of these models. One such subsystem seems to be the differentiation of the lint weight into computable components that can be combined in quantitative expressions of the lint quality. Efforts have been made

in this direction, and differentiation of yield and quality of the lint into their basic components is an example (Ramey, 1970; Worley *et al.*, 1974; Ramey and Worley, 1973; Turner *et al.*, 1979). If models which generate the lint quality can be elaborated and interfaced with the plant growth models, the subsisting terminological barrier between cotton growers and fiber technologists should progressively disappear.

SUMMARY

A comprehensive survey of lint development is provided with emphasis on the results of research done during the last ten to fifteen years on differentiation, elongation and secondary wall formation. The importance of these results for the fundamental knowledge of cell differentiation and cellulose biosynthesis is emphasized.

The various processes involved in the development of a typical lint fiber are discussed in the first part, while the variation of typical development is the subject of the second part, under the headings: "Cotton fiber populations" and "Lint production and lint quality".

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