Chapter

2.1

Morphology and Anatomy of the Cotton Plant

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Cotton: Origin, History, Technology, and Production, edited by Wayne C. Smith
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The cotton (*Gossypium hirsutum* L.) plant is a perennial with an indeterminate growth habit and is reputed to have the most complex structure of any major field crop (Mauney, 1984). Its indeterminate growth habit and sympodial fruiting branches result in a four-dimensional occupation of space and time that is difficult to analyze (Mauney, 1986). Furthermore, these characteristics ensure that vegetative and reproductive growth are occurring simultaneously, thereby increasing the difficulty of efficiently managing production practices such as fertilizer application and irrigation. Associated with this complex growth habit is an extreme sensitivity to adverse environmental conditions, reflected in excess fruit abscission. An understanding of cotton growth and development in commercial production is important in the continuing efforts of growers to produce lint and seed more efficiently and profitably. To properly design and implement crop-management programs that would enhance these parameters, the anatomy and morphological development of the cotton plant must be clearly understood. This chapter supplies an update on our current understanding of the structure and development of this economically important crop species.

PHENOLOGY OF COTTON

The growth, structure, and developmental patterns of the cotton plant have been covered in publications by Baranov and Maltzev (1937), Brown and Ware (1958), Dennis and Briggs (1969), Evans (1896), Hector (1936), Kerby et al., (1987), Mauney (1984), Oosterhuis (1990), and Tharp (1965). The physiology of the cotton plant has been described by Eaton (1955) and Carns and Mauney (1968) and, more recently, in the treatise edited by Mauney and Stewart (1986) which is currently being updated (Stewart et al., 1999). These publications and others were used in preparing the following description of the morphology and anatomy of the cotton plant.

Plant development in cotton proceeds through a number of stages, which for practical management reasons may be divided into four main growth stages (Landivar and Benedict, 1996): (1) germination and seedling establishment, (2) leaf area and canopy development, (3) flowering and boll development, and (4) maturation (Figure 2.1.1). A staging system devised by Elsner et al. (1979) based on plant growth increments has been used to describe phases of the cotton plant. Some researchers have further divided the first phase into germination and seedling establishment (Oosterhuis, 1990). Each stage involves the elaboration of new morphology and anatomy that builds upon the scaffolding and structures preceding it. Each elaboration is a product of genetics and environment. However, transitions between these successive stages are subtle and not always clearly distinguishable. Furthermore, each stage may have different physiological processes operating with specific requirements. If growers are aware of these stage-dependent differences and requirements in cotton growth, then many problems in crop management may be avoided, potentially resulting in increased yields and profits. Understanding each of the above stages involves a knowledge of the morphology and anatomy of the cotton plant, as well as an understanding of crop physiology (covered elsewhere in this publication). The main morphological events of a typical cotton plant from seed germination to boll maturation are presented in Figure 2.1.1 and described in the following text.

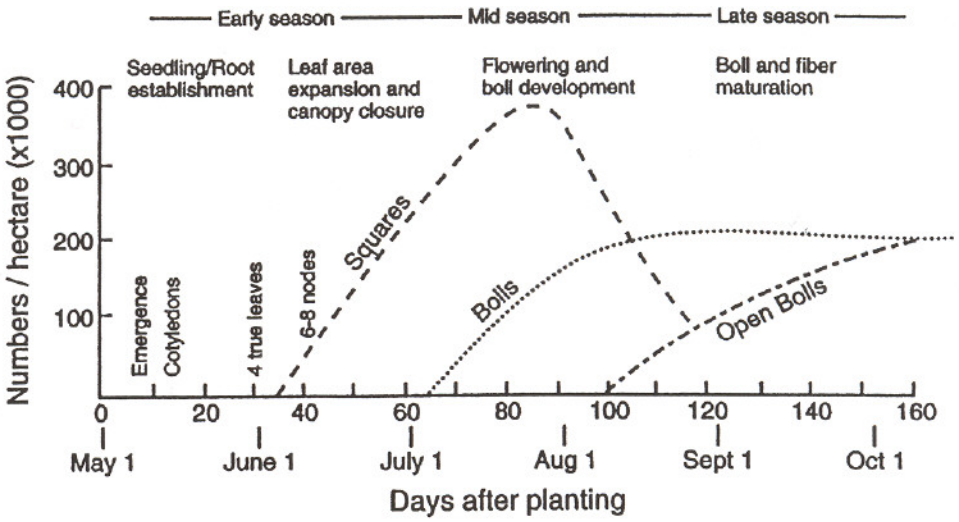


Figure 2.1.1. Typical seasonal development of cotton in the U.S. Cotton Belt showing the production of squares, bolls, and open bolls. [From Oosterhuis (1990).]

THE SEED AND GERMINATION

The Seed

The cotton seed is an ovoid, somewhat pointed, dark brown structure. The seed consists of a seed coat (testa), an embryo with two well-developed cotyledons, and remnants of the endosperm (Figure 2.1.2). Prior to ginning and delinting, the epidermal layer of the seed coat bears fibers or lint of two types: long lint fibers and short linters (or fuzz fibers). The embryo consists of a radicle, a hypocotyl, the two cotyledons, and a poorly developed epicotyl. The cotyledons, or seed leaves, eventually form the first green leaves, but initially they contain stored food which supplies the energy for germination and early development. There are usually about 8000 acid-delinted seed per kilogram.

Germination and Emergence

Germination begins with the entry of moisture within the first few hours through the chalaza (Tharp, 1965) and, later, through other parts of the seed coat into the embryo (Figure 2.1.2). Water is first absorbed through the chalaza and moves by capillary action around the internal periphery to the radicle of the embryo where it is taken up. There is no direct uptake by the cotyledons. Oxygen uptake occurs and respiration increases as the stored food reserves are utilized for energy and to build new cells and tissues. The seed/embryo swells as water is absorbed, causing the seed coat to

split at the pointed micropylar end. Under favorable conditions for germination, the radicle emerges through the micropyle within 2–3 days (Figure 2.1.3). The radicle forms the primary root that grows downward into the soil. The tissues between the radicle and cotyledons, the hypocotyl, grow rapidly, arching nearly 180° to form the "hypocotyl hook" near the cotyledons (Figure 2.1.3.). In most cotton genotypes, the root–hypocotyl transition can be identified by the absence of gossypol glands in the root. With continued expansion of the hypocotyl, the cotyledons and epicotyl are pulled up through the soil surface whereupon the hypocotyl straightens (Figure 2.1.3). Typically, the seed coat is shed and remains in the soil. Soil crusting due to surface compaction may hinder the emergence of the hypocotyl and cotyledons. No expanded true leaves are present at emergence.

Seed germination is favored by high soil oxygen concentration, adequate soil moisture, and soil temperatures above 18°C. Germination of cotton seed can begin when the mean daily soil temperature is 15°C or slightly below at seeding depths, but growth will be slow at these temperatures (Dennis and Briggs, 1969). Under favorable conditions, seedlings emerge above the soil in 5–10 days and require about 28–33 heat units with a base temperature of 15.5°C (Oosterhuis, 1990). Possible problems that hinder germination and emergence include poor seed quality, preemergence seedling disease, flooding, soil crusting, salinity, herbicide residue, and cool temperatures.

The cotyledons are carried 5–8 cm above the soil by the elongating hypocotyl before unfolding and expanding. During this phase the developing seedling is anchored in the soil by the rapidly expanding root system (Figure 2.1.3). After emergence and exposure to the light, the cotyledons become green due to chlorophyll and are capable of photosynthesis. Prior to this stage, the developing aerial portion of the seedling and the rapidly growing radicle have been dependent on assimilate stored in the embryonic axis and cotyledons. Much of the early development of the cotton plant is focused on

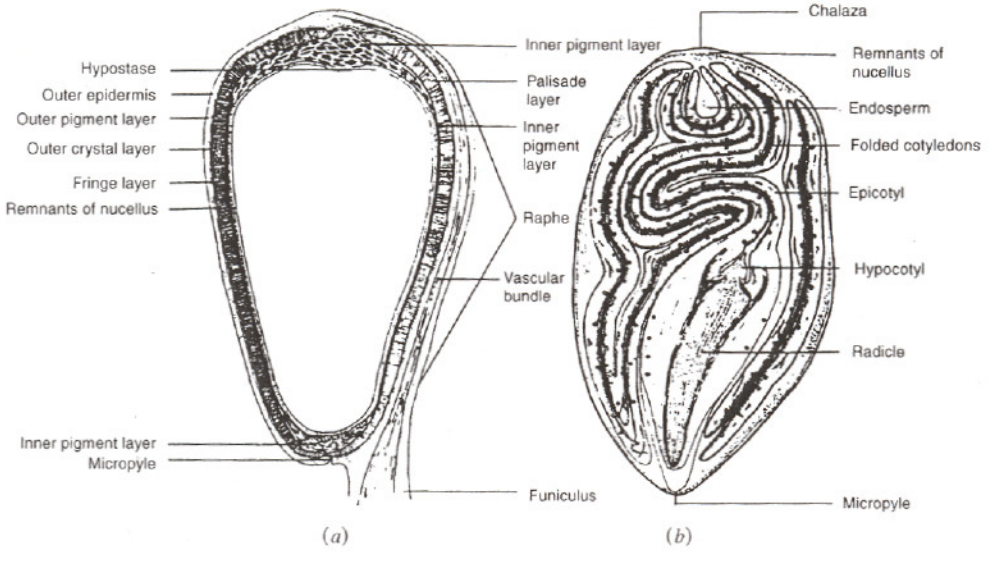


Figure 2.1.2. Structure of a mature cottonseed in longitudinal section. (*a*) Details of the seed coat. (*b*) Kernal showing internal structures. [Redrawn from Tharp (1965).]

the development of a substantial root sytem while growth of the above ground portion (first 4–5 true leaves) is relatively slow.

ROOTS AND ROOT SYSTEMS

Roots are often overlooked in production and research because of the difficulty in observing them and the lack of suitable techniques with which to analyze them. Even the classical and comprehensive coverage by Baranov and Maltzev (1937) of the development and structure of cotton paid the least attention to the roots, as did Mauney (1984) in his coverage of the anatomy and morphology of the cotton plant. Recent advances in methology (Upchurch and Taylor, 1990; Macfall, 1997) for studying roots *in situ* in the field have made cotton roots much more accessible to researchers and greatly increased our understanding of their growth and development. However, specific attention to cotton root anatomy is limited, with much of the referenced work having been done over 60 years ago (Hayward, 1938; Baranov and Maltzev, 1937).

Root Morphology

The development of the cotton root system under various different growing conditions has been described by a number of researchers (e.g., Balls, 1919; Collings and Warner, 1927; Brown and Ware, 1958; Taylor and Klepper, 1978; McMichael, 1986, Cappy, 1979). However, the effects of environmental stress on development and root responses to management inputs are less well understood. Cappy (1979) used a mini-rhizotron with a miniature camera and remote video monitor to observe and follow growth *in situ* during the growing season. Cotton root growth follows a typical sigmoidal curve and continues to grow and increase until about the time when maximum plant height is achieved soon after flowering (Taylor and Klepper, 1974) (Figure 2.1.4). At this time fruit begins to form and as the boll load develops, carbohydrates are increasingly directed toward the fruit which become the dominant sink for available

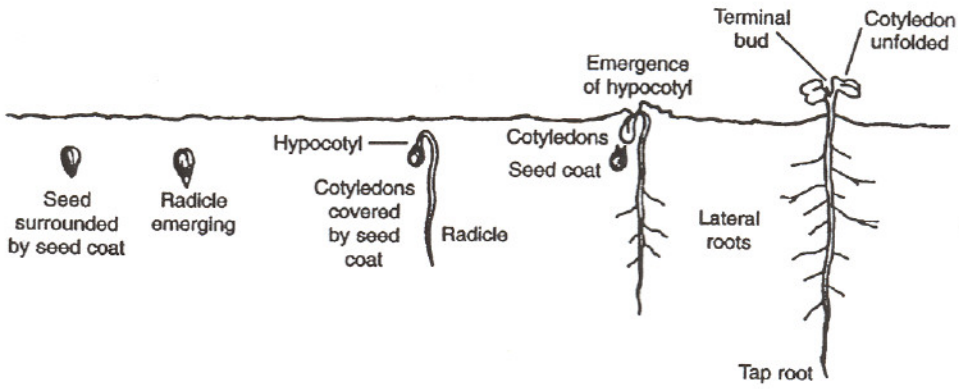


Figure 2.1.3. Germination and seedling emergence showing the early development of the radicle, taproot, and lateral roots. [From Oosterhuis (1990).]

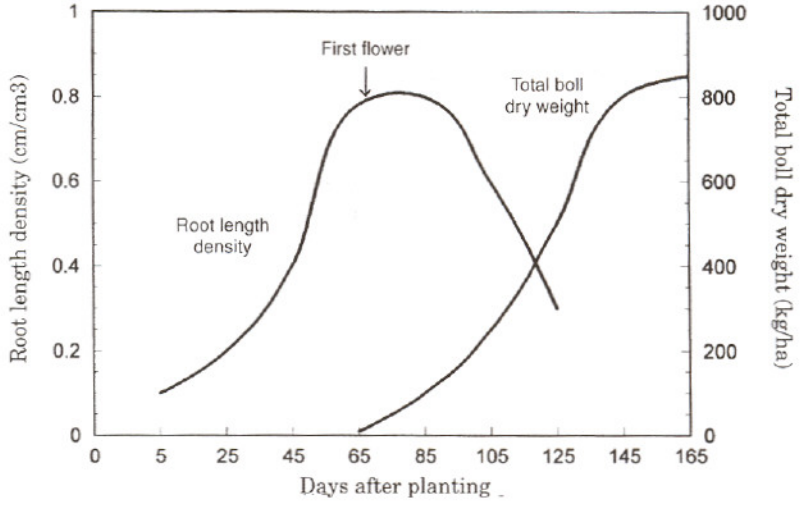


Figure 2.1.4. Typical growth pattern of cotton roots in relation to development of the boll load during a growing season.

photoassimilate. As older roots senesce, total root length begins to decline even though new roots continue to be formed (Hons and McMichael, 1986).

The radicle, or primary root, develops rapidly and is the first organ to emerge from the seed coat during germination. At temperatures below 10°C the root tip can be damaged permanently (Christiansen, 1968), a condition often referred to as "nub root." Weathered or deteriorated seeds can also lead to abnormal seedlings with nub root where part or all of the tap root fails to develop (Wiles and Presley, 1960) and because of a complete lack of cell division in the root tips.

The primary root, or taproot, penetrates the soil rapidly and may reach a depth of 25 cm or more by the time the cotyledons unfold (Taylor and Ratcliff, 1969). Root development during the early vegetative stage may proceed at the rate of 1–5 cm/day, depending on soil conditions, such that the roots may be 1.0 m deep when the above ground portion of the plant is only about 0.35 m (Figure 2.1.5). High water tables, compacted soils, and cool temperatures may result in much shallower root systems. The depth of root penetration depends on a number of factors, but in general the taproot can reach depths of over 3.0 m and can elongate at a rates of from less than 1 to over 6 cm/day (McMichael, 1986). A similar elongation rate has been reported for the lateral or secondary roots (McMichael et al., 1999).

Cotton has a "taproot" system, and therefore the shape of the root system, the volume of soil explored by the roots, and the overall root density are dependent on the development of secondary or lateral roots (McMichael et al., 1999). Numerous lateral roots proliferate outward from the taproot. These branch roots remain fairly shallow, usually less than 1 m (Hayward, 1938), but can extend outward from the taproot to a distance of over 2 m (Taylor and Klepper, 1978). Lateral root primordia generaly develop about 12 cm behind the primary root apex, with tertiary roots developing about 5 cm behind the secondary root apex (Mauney, 1968). The greater portion of the root system is located in the upper meter, but this is dependent upon soil moisture, soil physical structure, and plant vigor. Root distribution within the soil profile (root length

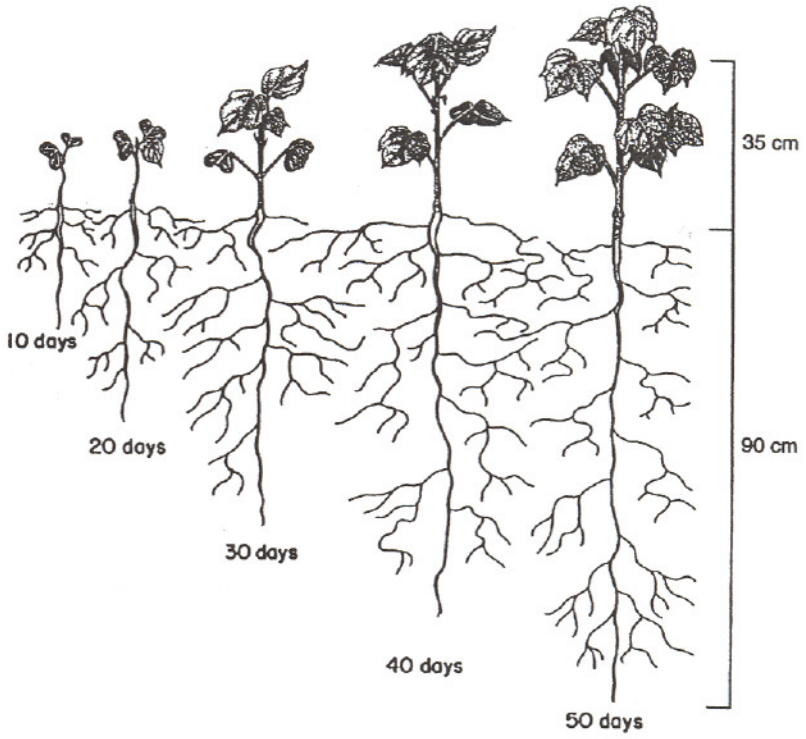


Figure 2.1.5. Root development of the cotton plant showing the extent of root growth compared to shoot growth up to 50 days after planting. [From Oosterhuis (1990).]

density) is usually about 3.7 cm/cm^3 of soil but can vary considerably with soil and plant conditions. The total root weight comprises approximately 10% (Jordan, 1983) of the total dry weight produced by the plant during the growing season. However, the total root length produced during the same time may be several hundred meters.

Anatomy of Cotton Roots

Cotton root anatomy was described by Hayward (1938), Baranov and Maltzev (1937), and Reinhardt and Rost (1995a, b and c). The anatomy of cotton roots is similar to that of a typical herbaceous dicotyledonous plant. The cotton plant has a primary root or taproot from which branch secondary, tertiary, and higher-order roots (Brown and Ware, 1985; Hayward, 1938; Spieth, 1933). The epidermis of a young cotton root, whether primary or branch root, is made up of a single layer of epidermal cells surrounding the cortex of unspecialized parenchyma cells. The endodermis, consisting of a single layer of cells with tangential suberin thickenings, forms the innermost layer of the cortex and surrounds the stele, which contains xylem and phloem tissues. The endodermis encloses a cell layer called the pericycle, which gives rise to lateral roots (Figure 2.1.6). The pericycle also eventually contributes to the protective outer layers of the root as the root ages and the endodermis and rest of the cortex and epidermis are sloughed.

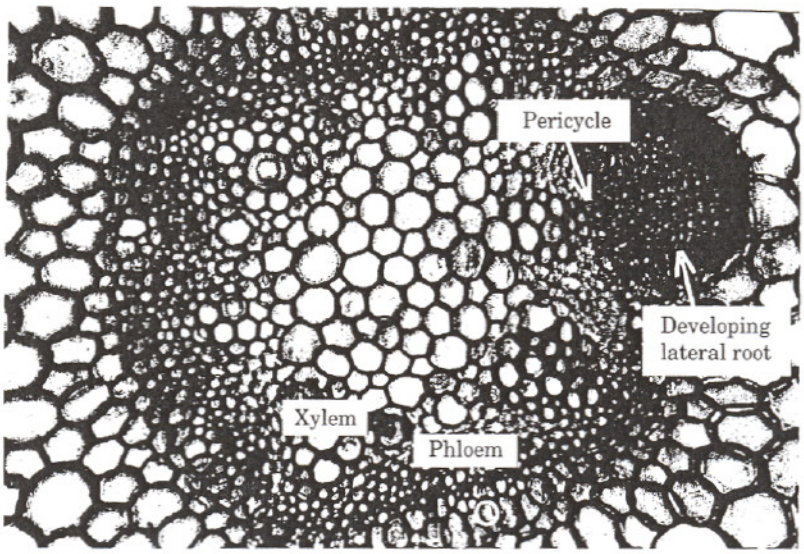


Figure 2.1.6. Growth of a lateral root from the pericycle at a pole of the primary xylem (×200). (Photograph by Oosterhuis.)

The typical cross-sectional anatomy of a mature cotton root is shown in Figure 2.1.7. In the mature root with primary growth, the sieve tubes and companion cells of the phloem are formed from the protophloem and metaphloem located between the xylem arms. As the root further matures a vascular cambium is formed which produces secondary phloem from its outer face and secondary xylem from the inner face. The pericycle is regenerated by tangential longitudinal cell divisions following vascular cambium formation. The secondary phloem and secondary xylem vascular tissues are arranged concentrically in a circle within the endodermis.

Root cross-sectional anatomy within the cotton germplasm collection has been studied (Oosterhuis et al., 1987; McMichael et al., 1985), and a wide range of diversity has been reported. The normal stelar arrangement in cotton and its wild relatives is tetrarch (four protoxylem poles), or in some cases pentarch. A higher number of xylem poles does occur, especially in cotton landraces (Oosterhuis and Wullschleger, 1989; McMichael et al., 1985). The range of vascular arrangements reported includes tetrarch, pentarch, hexarch and heptarch (Oosterhuis and Wullschleger, 1987). This higher number of poles was first thought to be involved with improved capabilities for water transport associated with increased xylem elements (Oosterhuis and Wullschleger, 1987), but is now understood to be more directly involved with a greater potential for improved lateral root growth (McMichael et al., 1987). A comparison of water flow in roots with tetrarch (cultivar Stoneville 506) and pentarch (wildtype T25) stelar arrangements showed no significant difference in water flow for the primary root (Oosterhuis and Wullschleger, 1987). An increased number of xylem strands could increase the ability to produce lateral roots (McMichael et al., 1985) which arise from the pericycle adjacent to each xylem pole in the stele (Figure 2.1.7). Lateral roots are arranged in rows opposite the xylem poles, and the number of rows varies according to the number of xylem poles present in the primary root. A direct correlation was

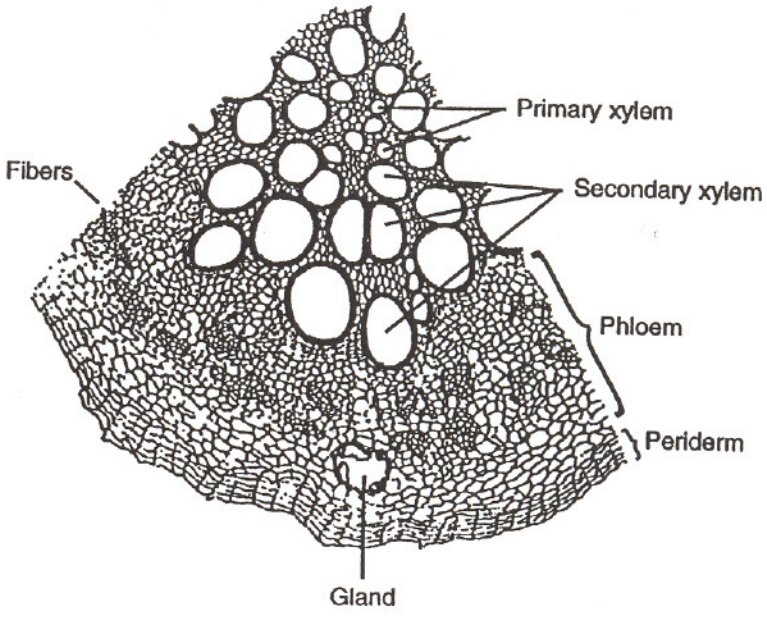


Figure 2.1.7. Transverse section of a portion of a tetrarch cotton root with secondary growth. The sequence of tissues and cell layers from the interior of the root to the exterior is: primary xylem (tetrarch arrangement); abundant secondary xylem; inconspicuous vascular cambium; abundant phloem with conspicuous parenchyma, fibers in bundles, a gland; and periderm. [Modified and relabeled from Baranov and Maltzev (1937).]

observed between the number of xylem poles in the taproots of cotton seedlings and the number of lateral roots produced (McMichael et al., 1987).

Progressive root xylem development is illustrated schematically and also with photomicrographs of transverse sections in Figure 2.1.8. Although some variation can be expected depending on the genotype and growing conditions, the general pattern seems clear. Most protoxylem elements are differentiated 2 cm from the apex but are relatively small in diameter (11 μm). At 6 cm from the apex, more protoxylem vessels are evident and appear wider (13 μm), and all possess well-defined secondary cell walls. At 10 cm from the apex all primary xylem elements are mature with clearly thickened cell walls, and a prominent central metaxylem vessel element is often observed (Figure 2.1.8). Although the stele is still in the primary state of growth 10 cm from the apex, it is beginning to show signs of vascular cambium development that will eventually lead to secondary growth.

Root hairs are outgrowths of individual epidermal cells that have undergone morphological transformations with no change in physiological function (Cailloux, 1972). Root hairs enhance the nutrient and water uptake capacity of plants and improve soil contact by increasing root absorptive area. They may increase root surface area 4–8 times (Dittmer, 1937) and increase root length 20-fold (Glass, 1989). A mantle of root hairs develops about 2 cm behind the root apex depending on growing conditions. Keino et al. (1998) reported that for a 7-day-old cotton plant, the taproot length varied between 9.5 and 14.8 cm, of which 40–66% of the root length

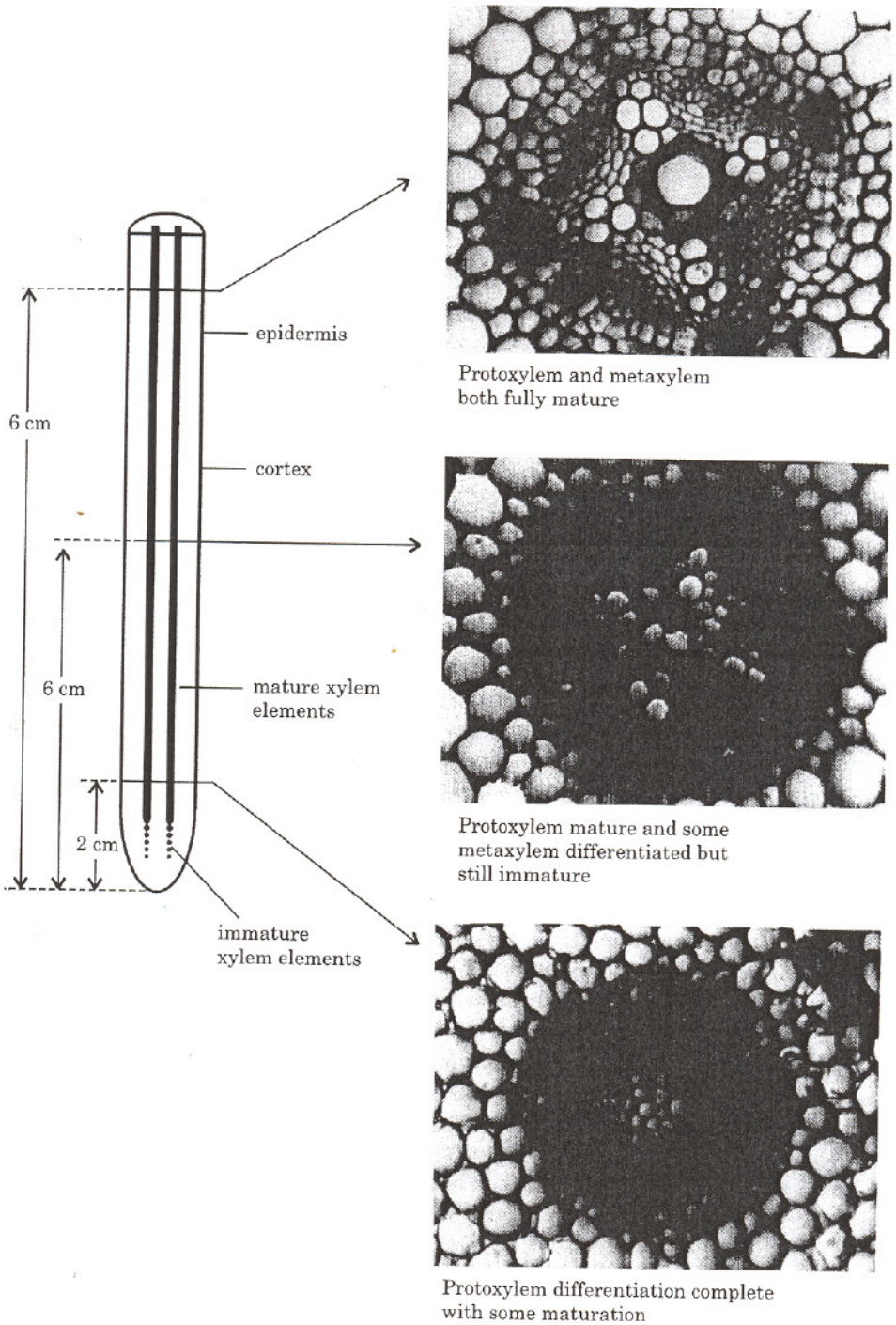


Figure 2.1.8. Schematic representation of a 10-day-old cotton root showing progressive xylem development behind the apex, accompanied by photomicrographs of transverse sections showing the xylem anatomy in detail (×225). [From Oosterhuis (1981).]

was occupied by root hairs. These authors also reported about 26–40 root hairs per millimeter of a 7-day-old taproot of cotton, with an individual length of 0.15–0.26 mm.

THE SHOOT SYSTEM

The shoot system of the cotton plant is made up of a main axis stem, leaves, buds, branches, and, ultimately, floral buds, flowers, and fruit (bolls). The prominent main stem, or primary axis, results from the elongation and development of the terminal bud or shoot apical meristem. The main stem consists of a series of nodes, where leaves are attached, and internodes. The main stem has an erect, indeterminate monopodial growth habit. The number of nodes, the length of the internodes, and the number and location of branches is determined by genetic and environmental factors including cultural practices.

The shoot system of a dormant cotton seed typically consists of the paired cotyledons, the primordium of the first true (foliage) leaf, and a dome of meristematic cells, the shoot apical meristem. Cotton shoot apical meristems are quite typical when compared to other dicotyledonous plants (Esau, 1977). The portion of the axis above the cotyledons, the epicotyl, is extremely reduced, and it comprises a single shortened internode and one node. Thus, all subsequent leaves, nodes, internodes, and axillary buds and branches develop following germination.

Seedling growth is relatively slow immediately following germination. Leaf initiation and expansion and internode elongation result in an unbranched plant with 4 or 5 expanded internodes about 1 month after planting (Figure 2.1.5). However, shoot growth during the subsequent 4 weeks is relatively rapid, so that by approximately 65 days after planting, 9–10 mature nodes and 5 or 6 elongated sympodial branches are present.

Monopodial and Sympodial Branching

Two types of branches may develop from the axillary bud associated with each true leaf: vegetative (or monopodial) and fruiting (or sympodial) branches (Figure 2.1.9). The number of nodes producing vegetative branches depends primarily on the environment and plant spacing. Vegetative branches are morphologically similar to the main stem; growth is from a single terminal bud, and branches arise some distance behind the indeterminate growing point. Two types of leaves arise on vegetative axillary branches: foliage (true) leaves and prophylls. Vegetative branches themselves do not bear flowers and fruits, but axillary buds borne along the vegetative branches may form sympodial branches, which do produce flowers and fruits (Figure 2.1.9). These vegetative branches normally arise from the main-stem nodes near the cotyledons (usually at main-stem nodes 3–5), and typically only one or two of these nodes show branch development, depending on growing conditions (particularly plant population density), in the absence of damage to the main axis shoot. Vegetative branches tend to grow in an upright orientation.

A vegetative branch meristem (axillary bud) initially produces a prophyll, an internode, and the first foliage leaf, which has an axillary bud associated with it. This is followed by formation of successive nodes with true leaves and axillary buds, separated by more or less conspicuous internodes. This contrasts with the first node of

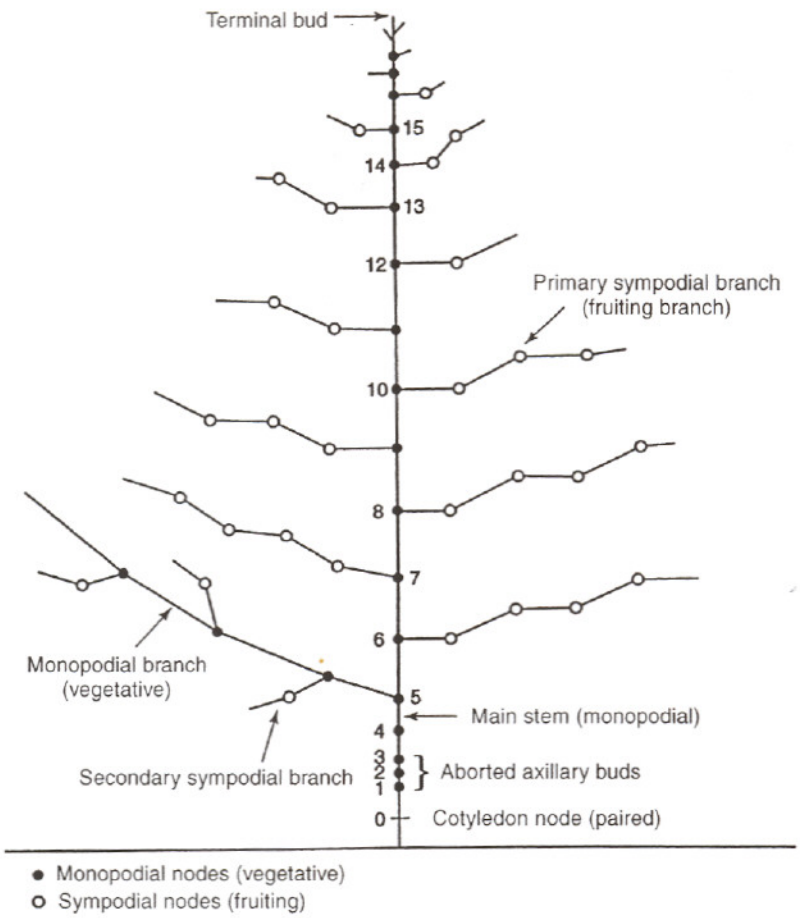


Figure 2.1.9. Diagrammatic representation of the cotton plant showing monopodial and sympodial branches. [From Oosterhuis (1990.)]

the expanding axillary bud, bearing the prophyll, below which no internode elongation occurs. Thus, the axillary bud of the prophyll appears to lie in the axil of the main-stem leaf.

Sympodial, or fruiting, branches arise from axillary buds of the main stem and from buds on vegetative branches. Fruiting branches are generally horizontal in orientation. The first fruiting branch normally occurs at the fifth to seventh node above the cotyledonary node on the main stem, and fruiting branch production usually continues to node 18–22, depending on production and growing conditions. All flowers and bolls produced on a cotton plant originate on sympodial branches. However, rebranched monopodial branches may produce up to 3–9% of the total yield (Jenkins et al., 1990). Once a plant begins producing sympodial branches, only under unusual environmental conditions will it revert to monopodial production above a sympodial node.

Internodes of cotton fruiting branches are often very short and nodes are crowded together, and axillary buds often show precocious development relative to subsequent

internode elongation. To understand sympodial (fruiting) branch growth and development, several points are helpful to keep in mind (Mauney, 1984, 1986): (1) Both types of leaves (prophylls and true leaves) occur on sympodial axillary branches, and both are associated with individual axillary buds (Figure 2.1.10 and 2.1.12). (2) A single axillary bud occurs in the axil of each prophyll or foliage leaf, and it may either remain dormant or develop into a branch. Depending upon where an axillary bud is located, and the phase of development of the plant, a bud may develop as a vegetative branch or a fruiting branch. (3) The shoot apical meristem of a fruiting branch terminates in a flower after first making a prophyll and then making a true leaf. This determinate growth of the fruiting branch apical meristem contrasts with the indeterminate growth of vegetative shoot apical meristems (main stem and vegetative branches). A vegetative branch continues to produce leaves until environmental factors cause growth to cease. (4) The sequence of structures and appendages produced by a sympodial meristem is: prophyll, internode, foliage leaf (with a bud in its axil), and flower (Figure 2.1.10). Formation of the flower terminates this axis, but growth continues in a typical sympodial fashion, with the activation of the bud in the axil of the foliage leaf. This bud makes the next "module" or the "renewal shoot" of the fruiting branch, consisting of a prophyll, an internode, a foliage leaf and associated axillary bud, and a terminal flower. This process is reiterated a variable number of times, resulting in the typical zigzag appearance of the fruiting branch due to the alternating positions of the axillary buds. Rather commonly, the bud in the axil of the prophyll will develop after 2–3 weeks into a short secondary sympodial branch bearing a single flower bud and leaf so that at maturity two capsules appear to occur at the same node. This occurs both at the main stem and at the first or second sympodial node. Fruiting branches in the middle region (nodes 7–10) on the main axis have 4–5 flowers, while lower and higher position fruiting branches bear progressively fewer flowers (Oosterhuis and Wullschleger, 1988).

New fruiting branches on the main stem are produced at intervals between 2.2 and 4.0 days, and nodes (fruiting positions) on a fruiting branch are produced at intervals between 5.8 and 8.5 days (Mauney, 1986). Kerby and Buxton (1978) reported for Arizona cultivars a 2.6-day interval at the beginning of flowering and 3.4 days 3 weeks later. This has been related to level of carbohydrate supply available to a position and fruit retention and fiber quality by position.

Stem Anatomy

Cotton has typical dicotyledonous stem anatomy (Figure 2.1.11) in which the primary vascular tissue is arranged in bundles around the pith (an eustele). Each collateral vascular bundle consists of primary phloem to the outside, primary xylem toward the interior, and residual procambium in a narrow band separating the primary xylem and primary phloem. The first-formed xylem (protoxylem) is closest to the center of the axis in a typical endarch arrangement. The pith consists of thin-walled parenchyma with small intercellular spaces. Three zones are usually recognizable in the cortex. Directly beneath the epidermis, the outer cortex consists of several layers of chlorenchyma; several layers of collenchymatous cells are found interior to this, and the inner cortex consists of parenchyma. Lysigenous glands containing terpenoid aldehydes are located in the outer cortex, and both unicellular and glandular hairs are found in the epidermis.

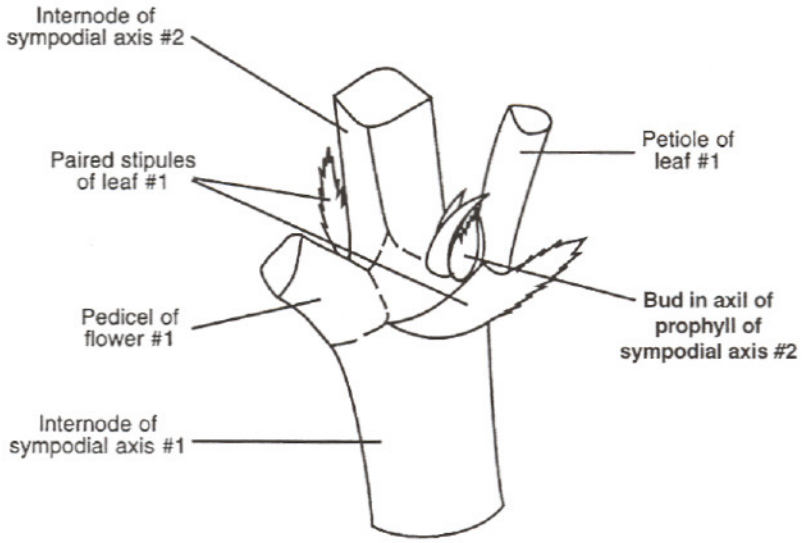


Figure 2.1.10. One node of a fruiting branch, showing parts of two sympodia. For simplicity, the internodes of the two successive sympodia have been labeled #1 and #2. The termination of sympodial axis #1 is the flower (#1) whose pedicel is shown, along with the leaf (#1) whose petiole is shown and its paired stipules. The bud in the axil of leaf #1 grew out to form sympodial axis #2, which had at its base a prophyll (not shown) associated with an axillary bud (also called the "secondary axillary"). (Modified from Hayward, 1938).

Limited secondary growth is found in stems of cotton grown as an annual. A periderm is formed as the epidermis and outer cortex become fissured and sloughed off during stem maturation. A large number of thick-walled fibers are found in the secondary phloem, while cells of the secondary xylem are not heavily lignified (Hayward, 1938), and the soft woody tissue disintegrates relatively quickly.

Leaves

The arrangement of the leaves on a cotton stem (phyllotaxis or phyllotaxy) is spiral, with one leaf at each node, and each successive leaf attached 3/8 of a turn away from the preceding or following leaf. Because branches arise in the axils of leaves, branches are also spirally arranged and show the same 3/8 pattern. The phyllotactic spiral on cotton stems may be clockwise (dextrorse) or counterclockwise (sinistrorse) when viewed from the top, and it is apparently determined at random because there is an approximately 1:1 ratio of the two forms. The direction of the spiral on branches is unaffected by the direction of the spiral of the main stem from which the branches develop. Infrequently, a stem may be observed in which the phyllotactic spiral has reversed direction (Mauney, 1984).

Cotton plants bear three types of leaves: cotyledons, prophylls, and foliage leaves (also termed true leaves) (Mauney, 1984). Leaf shape in cotton is determined by the developmental age of the shoot and by several genes which affect leaf lobing (Dolan and Poethig, 1991, 1998a, 1998b). Cotyledons, or seed leaves, occur oppositely on

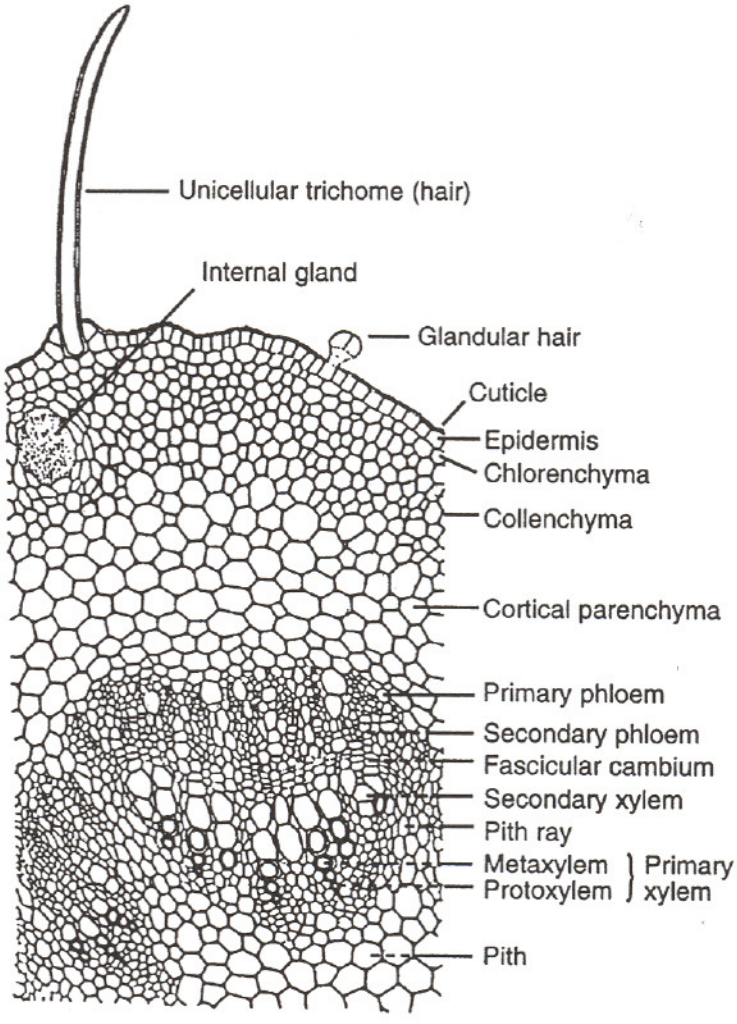


Figure 2.1.11. Transverse section of young cotton stem. [Modified from Hayward (1938).]

the embryonic shoot, and they quickly expand and become green and photosynthetic following seedling emergence. The two cotyledons are kidney-shaped and approximately 6 cm long and 4 cm wide when fully expanded (Figure 2.1.12). At each of the first few nodes above the cotyledons, a simple, entire, heart-shaped foliage leaf arises. Leaves at successive nodes are increasingly palmately lobed, typically with three to five lobes, and 10–15 cm wide. Lobing varies greatly among genotypes, ranging from little or no indentation in some wild types to complete indentation in some "superokra-leaf" cottons. All foliage leaves typically have paired appendages, called stipules, at the base of the petiole. The stipules are narrow tapering structures approximately 7–10 mm in length. Stipules are usually marcescent and short-lived (Hayward, 1938), and they probably serve to protect the leaf primordium in the bud. Foliage leaves with stipules are borne on the main-stem axis, on lateral monopodial branches, and on sympodial branches. Prophylls are the first foliar appendages produced on axillary

branches (both vegetative and fruiting). Typically a bud has only a single prophyll. Prophylls in cotton are small (2–5 mm in length), tapering, green, and inconspicuous. Prophylls lack stipules, and they are often confused with the stipules of foliage leaves. Like the stipules, prophylls usually become dry and shriveled after bud expansion.

Growth of true leaves is relatively slow at first compared to root growth, such that at 1 month after planting only about 4 or 5 true leaves may be unfolded and visible. The time from emergence to full true leaf expansion will be lengthened under conditions of low temperaures, low seedling vigor, seedling diseases, inadequate soil moisture, improper dosage or application of herbicides, fertilizer salt damage, low oxygen, and thrip injury. True leaves arise from the main stem (main-stem leaves) and from the sympodial/fruiting branches (so-called sympodial leaves) (Figures 2.1.12 and 2.1.13). The main-stem leaves mainly contribute to vegetative development including the main stem and sympodial branches (Oosterhuis and Urwiler, 1988), but also to boll development (Brown, 1968; Wullschleger and Oosterhuis, 1990). On the other hand, the sympodial leaves are almost exclusively associated with carbon partitioning to the boll (Constable and Rawson, 1980; Ashley, 1972). The average longevity of an individual leaf is about 65 days (Wullschleger and Oosterhuis, 1990). The leaf petiole, which is often analyzed to estimate plant nutrient status, is about as long as the leaf is wide.

Leaf Area and Canopy Development

Vegetative development proceeds with the growth of the true leaves on the main stem (Figure 2.1.13) and with the development of the foliated monopodial and sympodial branches (Figure 2.1.9). Leaf area continues to increase and typically follows a sigmoidal growth pattern. The distribution of total leaf area by main-stem node up the main stem was described by Oosterhuis and Wullschleger (1988) for both main-stem leaves and sympodial leaves. The total amount of leaf area, commonly referred to as the "leaf area index" (LAI), is the amount of leaf area per unit area of land. Total LAI increases slowly during the the first 6–7 weeks following emergence, and then more rapidly during early fruiting and canopy closure. During the early vegetative period, root development predominates, whereas squares and flowers develop during the later vegetative period. It is imperative that leaf area development progresses during this period so as to maximize the utilization of incoming solar radiation for photosynthesis

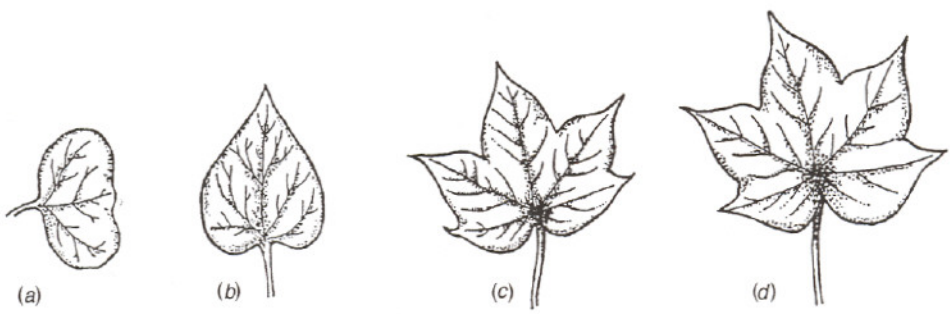


Figure 2.1.12. Cotton leaves. (*a*) Cotyledon (seed leaf), (*b*) first main-stem true leaves, (*c*) sympodial leaf of a fruiting branch, and (*d*) main-stem leaf. Not drawn to scale. [From Oosterhuis (1990).]

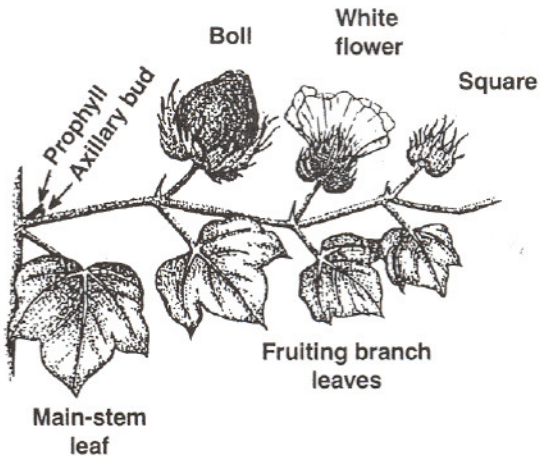


Figure 2.1.13. Cotton square, flower, and boll on a sympodial branch. Also shown are the prophyll, axillary bud, main-stem leaf, and sympodial leaves.

as soon as possible. Early canopy closure also improves weed control, and it decreases soil evaporative losses by confining evaporation to that occurring by transpiration, thereby providing the plant more control over water loss.

Main-stem leaves are the only true leaves present during the first 5 or 6 weeks after planting, after which the sympodial leaf area increases rapidly and exceeds the main-stem leaf area soon after first flower (Oosterhuis, 1990). Agronomically, main-stem leaves are the predominant leaves in the plant apex, and thus serve an important role in light interception and as a primary target for egg laying by certain insects. Main-stem leaf area reaches a maximum prior to first flower and remains relatively constant thereafter at about 40% of total, whereas sympodial leaf area continues to increase for an additional month when they constitute about 60% of the total leaf area (Oosterhuis and Wullschleger, 1988; Mutsaers, 1983).

Leaf Anatomy

The cotton leaf shows typical bifacial or dorsiventral organization, with a single layer of palisade parenchyma below the epidermis on the upper (adaxial) side of the blade and spongy parenchyma below the epidermis on the lower (abaxial) side (Figure 2.1.14). Stomata are present on both the adaxial and abaxial epidermal layers, but are more numerous on the lower leaf blade surface. A cuticle is found on both upper and lower epidermal layers, the details of which are discussed below. Internal lysigenous glands occur in all interveinal areas of the leaf and in the ground tissue of the midrib, toward the abaxial side. A nectary occurs on the abaxial surface of the midrib, and in a few genotypes nectaries occur on the abaxial surface of the two major lateral veins as well. The main veins have rib-like projections on the adaxial surface, consisting of collenchyma located directly beneath the epidermis. Leaf vascular bundles are collateral. The xylem, with its orderly files of cells, is toward the upper leaf surface,

while the less regularly ordered phloem is toward the lower. In main veins, a narrow band of residual procambium is evident between the xylem and phloem. In cross-sectional view, the petiole of the cotton leaf is circular to oval in shape, with the vascular bundles arranged in a ring of four or five large bundles and several smaller ones (Hayward, 1938). The cotton petiole has swellings (pulvini) at the base and distal ends which are associated with nyctinastic leaf movements. Lysigenous glands are also found in the cotton petiole.

Both surfaces of the cotton leaf, immediately above the epidermal cell layer, are covered with an amorphous layer of cuticle with numerous epicuticular wax ridges (Wullschleger and Oosterhuis, 1989; Oosterhuis et al., 1991b) (Figure 2.1.15a). The cuticle is composed of cutin impregnated with wax arising from the outer tangential walls of the epidermal cells (Bondada et al., 1994). The cuticle reduces water loss and constitutes the first line of defense against adverse environmental stresses including rainfall and chemical penetration. Cotton leaves generally have a thick waxy cuticle, with numerous stomata, and and a few unicellular and glandular trichomes on the surface (Figure 2.1.15a). The leaf epiculticular wax layer in cotton is about 30 μm thick, although the thickness has been shown to increase by as much as 30% with exposure to water deficit (Oosterhuis et al., 1991a; Weete et al., 1978). Leaf glaucousness (waxiness) is a characteristic that has been cited as a plant adaptation to drought (Johnson et al., 1983). Environmental factors such as radiation, temperature, humidity, and water stress have been shown to affect the amount of surface wax in plants.

The stomata in cotton have a prominent epicuticular ledge partially covering the stomatal pore (Figure 2.1.15b) which has been associated with drought tolerance. An internal cuticle extending from the outside of the stomate through the stomatal pore of the gaurd cells over the first few mesophyll cells of the substomatal cavity has been reported (Figure 2.1.15c) (Wullschleger and Oosterhuis, 1989). The role of this internal cuticle has also been related to increased drought tolerance. The waxy cuticle covering the leaf is of similar form and composition to that covering the boll (Figure 2.1.15d). Both leaf and boll cuticle thickness will increase with organ age (Bondada et al., 1994). Incidentally, the cotton fiber is also covered with a cuticle (DeLanghe, 1986).

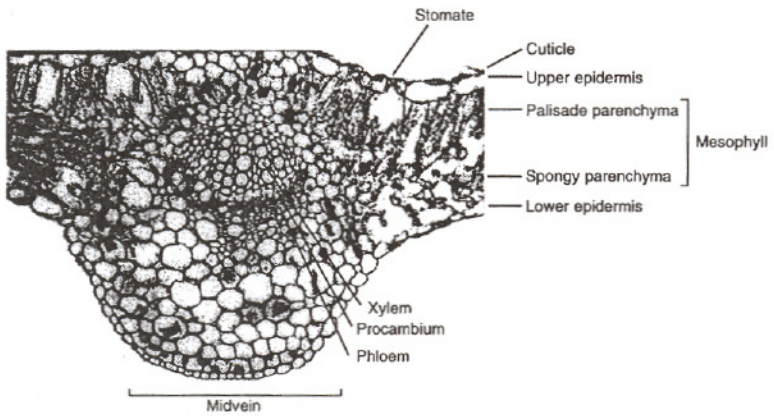


Figure 2.1.14. Cross section of a mature cotton sympodial leaf in the mid-vein region showing the anatomy. [From Oosterhuis et al. (1991b).]

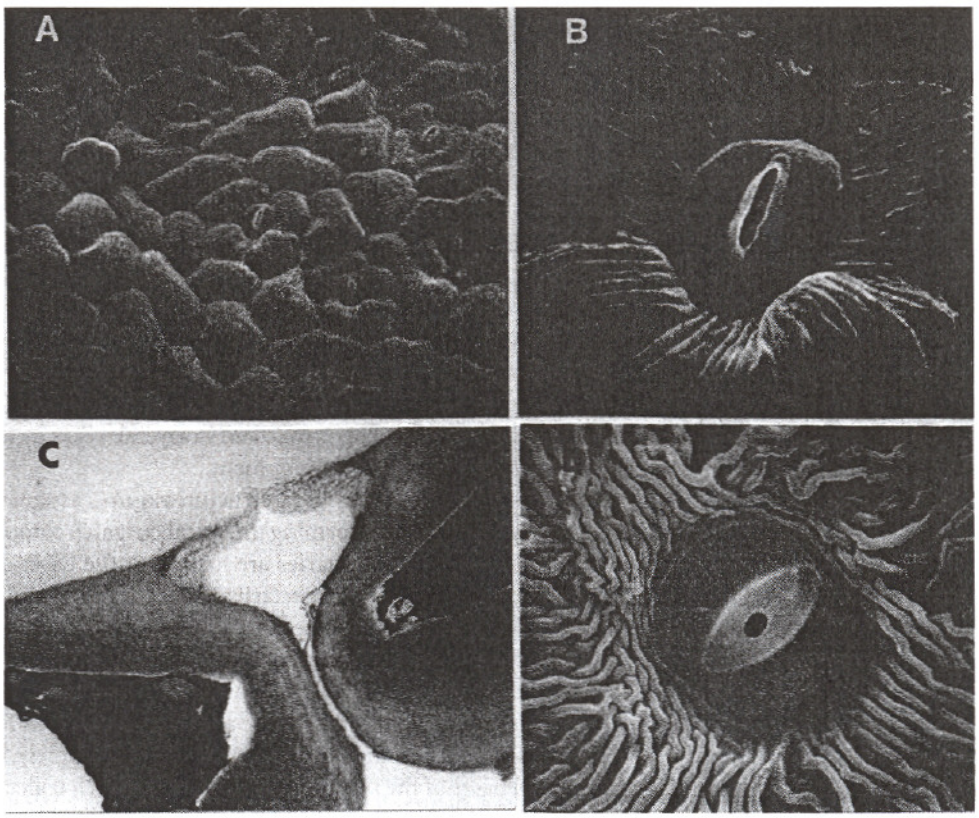


Figure 2.1.15. The cotton cuticle . (*a*) Adaxial sympodial leaf surface scanning electron micrograph (×700), (*b*) stoma with epicuticular wax ridges (×3000), (*c*) cross section of a stoma showing epicuticular ledges and internal cuticle (×10,000), and (*d*) boll cuticle showing buildup of wax and stomatal pore partially occluded (×3500) [*a* is from Oosterhuis et al. (1991a); *b* and *c* are from Wullschleger and Oosterhuis (1989); *d* is from Bondada et al. (1994).]

REPRODUCTIVE STRUCTURES

Flowering Pattern

Cotton has a distinctive and predictable flowering pattern. The first flowers to open are low on the plant, usually at main-stem nodes 6 or 7 and at the first position along a fruiting branch. About 3 days elapse between the opening of a flower on a given fruiting branch and the opening of a flower at the same relative position on the next higher fruiting branch (known as the vertical flowering interval). On the other hand, the time interval for the development of two successive flowers on the same branch is about 6 days (horizontal flowering interval). The order is thus spirally upward and outward. Flowers will continue to be produced until defoliation or frost, if the plant is actively growing and has not gone into cutout.

The shedding or abscission of squares and young bolls is a natural occurrence in cotton that is accentuated by adverse environmental conditions, including extended

overcast weather, extreme temperatures, water stress, and insect damage. A typical daily square production pattern and the ensuing bolls that are set is shown in Figure 2.1.1. Flowers typically are not shed. A cotton plant commonly sheds about 60% of its squares and young bolls under typical crop growing conditions. Excessive shedding of squares or bolls can result in significantly altered plant morphology by effectively increasing vegetative growth. This is because fruit removal changes the major "sink" for assimilates from the squares and bolls to vegetative components such as the terminal buds and leaves, resulting in rank growth.

Flowering and Boll (Fruit) Development

Reproductive growth commences about 4–5 weeks after planting, with the formation of floral buds in the apical part of the plant. This is followed in several weeks by flower opening (anthesis) and the start of fruit (boll) development.

Floral buds appear first as small, green, pyramidal structures known as squares. A square is composed of three large green bracts, forming the epicalyx, which completely enclose the developing flower. Three to six nectaries are located at the bases of the bracts (Hayward, 1938; Beasley, 1975): three floral nectaries inside the bracts and three extrafloral (involucral) nectaries located at the bases of the bracts on the outer side. Inside the bracts, floral organs are initiated sequentially beginning from the outside in (Shi et al., 1988). Sepals are the first floral organs initiated, followed by petals, stamens, and carpels. The structure of a cotton flower at anthesis is shown in Figure 2.1.16. The five sepals are fused most of their length to form the obliquely lobed calyx which tightly encloses the bases of the five conspicuous petals which collectively form the corolla. The corolla appears to be polypetalous (distinct petals) but it is, in fact, sympetalous (petals fused at the base). Floral nectaries are part of the adaxial epidermis at the base of the calyx (Hayward, 1938). The staminal column is composed of numerous filaments which are fused to the corolla and with each other along most of their length. Distinct filaments are exerted in pairs along the length of the staminal column, and each bears a two-lobed anther. The staminal column surrounds the style which, together with the 2- to 5-lobed stigma and ovary, constitute the female part of the flower (also called the pistil or the gynoecium). The ovary is superior and composed of three to five united carpels each with several ovules. One carpel forms one locule (or loc). Cotton ovaries exhibit axile placentation, with two rows of ovules in each locule. Each locule contains some 8–15 ovules, the number of which varies with variety and growth conditions during flower development. However, not all of these ovules develop into mature seed; there is usually an average of about eight seeds per locule.

The length of time between the first appearance of a given square (i.e., pinhead square size) and anthesis (white flower stage) is approximately 25 days (Tharp, 1965). Upland cotton (*Gossypium hirsutum*) flowers are creamy white on the day of flowering (when anthesis and pollination occur), but petals turn pink-red the following day and abscise at the base 1 or 2 days later. Pima cotton (*G. barbadense*) flowers are yellow at anthesis but also turn pink.

Cotton flowers open at or near dawn and remain open for only a single day. Anthesis is usually followed shortly by the dehiscence of anthers soon after the petals open, although high humidity or cool temperatures can delay this by 2 to 3 hours.

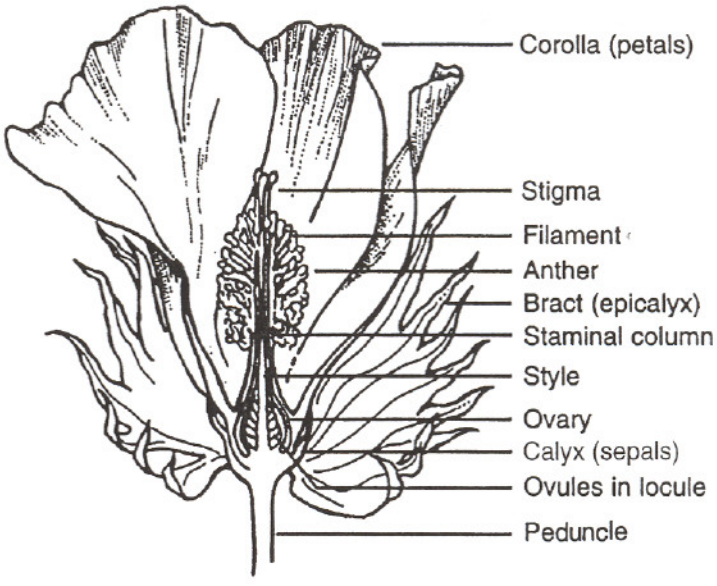


Figure 2.1.16. Longitudinal section of a typical cotton flower on the day of anthesis. [From Oosterhuis (1990).]

Pollination, the transfer of pollen from the anthers to the stigma, occurs shortly after anthesis. In the absence of insect pollinators, cotton flowers are self-pollinated; but when pollinators such as *Bombus* sp. are present, cross-pollination can be significant (i.e., up to 50–80%). The stigma becomes receptive shortly after the flower opens.

Cotton pollen is more or less spherical and very spiny. Cotton pollen is shed from the anthers at the two-celled stage, so that the immature male gametophyte (microgametophyte) consists of a tube (or vegetative) cell and a generative cell. Following adhesion of pollen grains to the stigma, the pollen germinates and a pollen tube rapidly penetrates the stigma and grows the length of the style into the ovary. The generative nucleus divides shortly after pollen tube emergence to form two sperm cells. The tube emerges from the placental tissue and enters the micropyle of an ovule. The amount of time required for the tube to effect fertilization can be as little as 12 hours following pollination, or it can more than 24 hours. Temperature is the primary determining factor.

Cotton ovules are anatropous, bitegmic (two integuments), and crassinucellate. The female gametophyte (megagametophyte) is the monosporic, eight-nucleate (*Polygonum*) type, which is the most widespread type in the angiosperms. Thus, the mature female gametophyte (also termed the embryo sac) consists of seven cells, six of which are uninucleate (egg cell, two synergids, and three antipodals) and the binucleate central cell. Readers are referred to Joshi et al. (1967) for a detailed description of micro- and megasporogenesis and micro- and megagametogenesis in cotton.

Fertilization in cotton is among the best studied in flowering plants, based largely on the classical work of Jensen and Fisher (1968) and Fisher and Jensen (1969). The pollen tube enters the micropyle of the ovule and then enters the embryo sac by penetrating one of the two synergids that lie adjacent to the egg cell at the micropylar

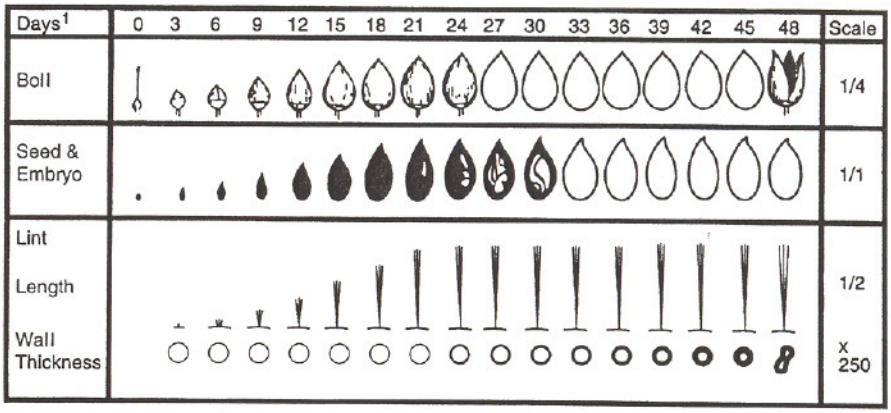
end of the embryo sac. At this point, the pollen tube discharges its contents, including the two male gametes and the vegetative nucleus, into the receptive synergid, through a definite pore formed near the tip of the pollen tube. By some mechanism still unknown, the two male gametes are liberated from the degenerating synergid and enter the egg and central cell of the embryo sac. Double fertilization is accomplished by the fusion of one sperm nucleus with the egg nucleus and fusion of the other sperm nucleus with the two nuclei of the central cell. The products of double fertilization are the zygote (egg + one sperm) and the primary endosperm nucleus (two central cell nuclei + one sperm). Initially, the new zygote shrinks in size and appears quiescent, but by 2–4 days after anthesis the zygote has divided (Joshi et al., 1967). Rapid divisions of the triploid primary endosperm nucleus begin almost immediately to form a multinucleate liquid endosperm (also called a free nuclear endosperm). After 10–12 days the endosperm becomes cellular as each nuclear division is now followed by cell wall formation. Enlargement of the young capsule (boll) begins with fertilization (Mauney, 1984). Embryogeny of cotton corresponds to the asterad type (Joshi et al., 1967; Johansen, 1950), and endosperm formation is of the nuclear type (Joshi et al., 1967).

The bracts of the square are the most evident feature of a young boll, and they reach their maximum size at about anthesis (Zhao, 1997). They function in protection and as a source of photoassimilates. These bracts completely enclose the developing floral bud until the corolla forms a "candle" on the day prior to flowering. The bracts continue to enclose the developing boll for about a week after anthesis.

The capsule is thick and leathery at maturity, and it rapidly dries to become brittle and brown. The cotton fruit, or boll, consists of three parts: the capsule (the bur), the seeds, and the fiber. In modern cultivars, the first mature fruit splits open along the partitions between locules at about 40–45 days after pollination and is termed a septicidally dehiscent capsule. Balls (1915) presented a diagrammatic representation of the developing boll in relation to corresponding changes in development of the seed and fiber (Figure 2.1.17). The seeds are attached to the central column of the boll (Figure 2.1.18), and there are usually about eight seeds per locule. The pattern and distribution of differential cell wall thickenings, including those of the vascular bundles, cause the capsule walls to bend backwards upon drying.

Boll Distribution on the Cotton Plant

The distribution of bolls on the plant varies due to abscission from physiological and environmental causes (Guinn, 1982; Benedict, 1984). Abscission of squares and bolls is a natural and necessary process because the plant is incapable of nurturing to maturity all the squares initiated. Boll retention declines later in the season as available photoassimilate becomes limiting. Fruiting site position within the canopy influences boll retention and boll development (Jenkins et al., 1990). Plant diagrams are used to "map" the positions of bolls on the plant (Figure 2.1.19) and are useful management tools to follow development and assess the success of production inputs. Oosterhuis et al. (1996) published an explanation of terminology used in describing plant mapping and the associated plant structures. A large percentage (>70%) of the total yield is derived from the central portion of the canopy, approximately between main-stem nodes 9 and 14 (Jenkins et al., 1990), depending on the length of the growing season, plant density, nutrition, insect control, and water availability. These nodes



[1] Days past anthesis

Figure 2.1.17. Diagrammatic representation of the developing boll in relation to corresponding changes in development of the seed and fiber from flowering (0 dpa) to open boll (48 dpa). [From Balls (1919).]

coincide with the distribution of maximum leaf area within the canopy (Oosterhuis and Wullschleger, 1988). Fewer bolls are produced above these nodes, they tend to take longer to mature and are smaller in size, and they are inferior in seed and fiber quality. The decline in vigor of the fruiting structures at higher nodes is evident in the buds prior to flowering (Holt et al., 1994).

Seed and Seed Coat

The general structure and development of the cotton seed and seed coat have been described and discussed by several investigators. Useful sources include Reeves (1937), Hayward (1938), Pearson (1939), and Joshi et al. (1967). Only a brief recapitulation will be presented here.

The cotton ovule is anatropous and bitegmic (Figure 2.1.2). Both integuments form the micropyle, which may be straight or zigzag in longitudinal section. The raphe, formed by fusion of the funiculus with the outer integument, runs along one side of the ovule. A network of vascular tissue extends throughout the outer integument but not the inner integument. The seed coat of the mature ovule develops from both integuments, which differentiate and eventually desiccate. At maturity the outer epidermis of the outer integument consists of fuzz and lint fiber cells (specialized epidermal cells), guard cells, and epidermal cells. Beneath this uniseriate layer lies the multicellular ground tissue which is three to four cells thick near the micropyle but several cell layers thicker at the chalaza. At the chalazal end itself the cells are loosely packed into a spongy tissue. The vascular tissue of the ovule traverses the ground tissue of the outer integument (Figure 2.1.20). The ground tissue is also termed the "outer pigment layer" because of the dark color of cellular contents, apparently tannins, in this region (Pearson, 1939). The inner epidermis of the outer integument, typically a single cell layer thick, develops thickened walls and frequently contains calcium oxalate crystals. This layer is also called the "colorless layer" or "crystal layer."

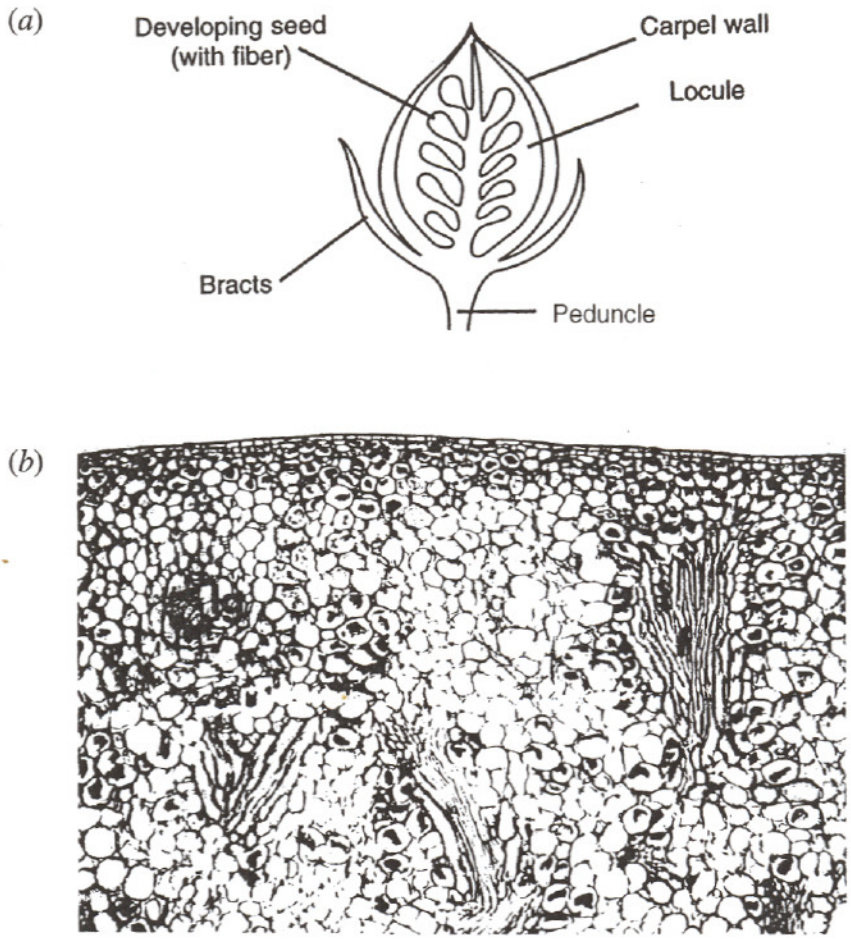


Figure 2.1.18. Internal details of a cotton boll. (*a*) Longitudinal section of a mature cotton boll showing the seeds and fibers (actual size). (*b*) Light micrograph cross-section of the boll wall showing the pericarp with fibers (f) and lysigenous gland (lg) (×100). (Figure *b* by B. R. Bondada).

The mature inner integument is also highly differentiated (Figure 2.1.20). Cells of the outer epidermis of the mature inner integument are radially elongated with thickened walls. This layer gives strength and hardness to the seed coat; it is sometimes termed the "palisade layer." The outer epidermis of the inner integument is continuous around the ovule except for a circular break or "anchor ring" located at the chalazal end of the ovule. At least some cells of the ground tissue of the inner integument have dark contents and are somewhat crushed and disorganized. Although typically of greater thickness, this tissue resembles the ground tissue of the outer integument ("outer pigment layer") and has been termed the "inner pigment layer." Some authors (Joshi et al., 1967) have also reported the presence of an inner colorless zone, also part of the ground tissue of the inner integument. The innermost layer of the inner integument, the inner epidermis, often separates from the rest of the seed coat at maturity, adhering, instead, to the remains of the

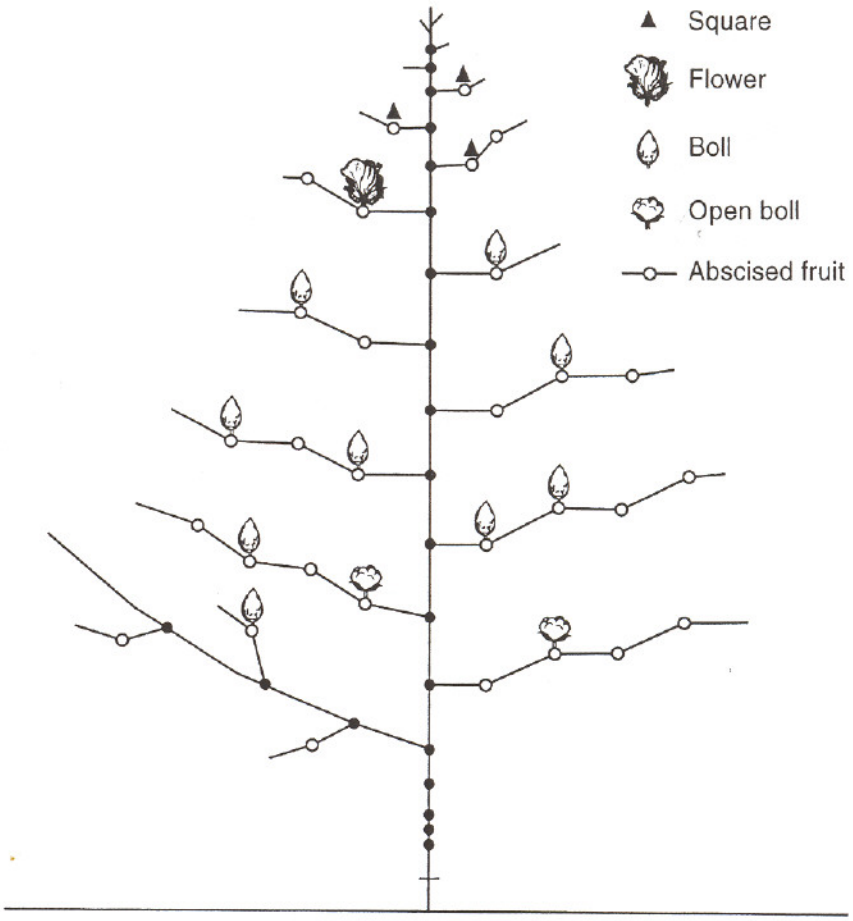


Figure 2.1.19. Boll distribution on a plant at maturity.

nucellus and endosperm surrounding the embryo. The inner epidermis of the inner integument is also known as the "fringe layer," cells of which are usually somewhat elongated.

Seed coat anatomy is significantly different in the chalazal region compared to the sides of the seed. The interruption in the pallisade layer described above is associated with the absence of an outer integument inner epidermis (colorless layer) and an inner integument inner epidermis (fringe layer). In addition, anatomically defined inner and outer pigment layers are lacking in this region. In the place of the "normal" seed coat cells and tissues, Pearson (1939) reported a core of compact cells filling the hole in the palisade layer, surrounded on either side by "spongy tissue" comprised of branched parenchyma cells and abundant intercellular spaces. She concluded that this "chalazal plug" and adjacent tissues constitute a zone of weakness in the seed coat, and its existence could account for the tendency of cotton seeds to rupture at the chalazal end during ginning and other processing steps. This region is also the first to imbibe water leading to germination (Tharp, 1965).

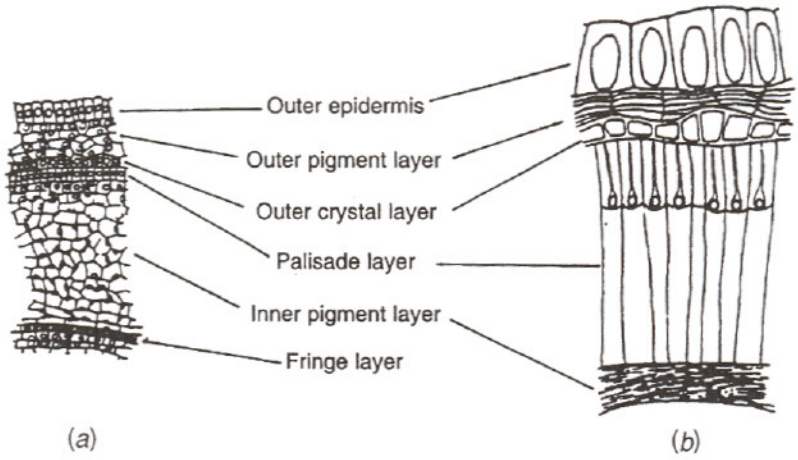


Figure 2.1.20. Seed coat. (*a*) Cellular diagram of tissues and cells of developing seed coat, showing anatomy at the day of fertilization. (*b*) Cellular diagram of tissues and cells of mature (48 days after fertilization) seed coat of upland cotton. [Modified from Pearson (1939).]

Fibers

The development of the cotton fiber is covered in greater detail in another chapter in this volume, so this is a necessarily brief account of the origin of these economically important plant "hairs."

Cotton fibers are epidermal trichomes (hairs) that arise from the protoderm of the ovule. The protoderm is a primary meristem of the plant and, consequently, continues to undergo mitotic cell divisions for a number of days following anthesis (Farr, 1931; J. M. Stewart, personal communication). In addition to hairs, cells of the protoderm differentiate and mature as stomata (guard cells and pore) and epidermal cells (Stewart, 1975).

The first wave of fiber initiation occurs shortly before anthesis (in pima cotton) or shortly after anthesis (in upland cotton), and it is recognizable by the domed swelling of apparently randomly located cells of the protoderm (see however, Holt and Stewart, 1994). Fiber initials appear first in the chalazal region of the ovule (top of the raphe), while fiber development may be delayed at the extreme micropylar end by 2–3 days (Stewart, 1975). A second wave of fibers is initiated 5–10 days following anthesis, forming the fuzz fibers, or linters (Lang, 1938).

Fiber growth over the first 24–48 hours is considered to be nonpolar or isodiametric, in that the fiber initials simply enlarge to form nearly spherical balloon-like protrusions from the ovule surface. By the second day following fiber initiation, fiber cells show distinctly polar growth, toward the micropylar end of the ovule and elongate to form tubular outgrowths, with either blunt or tapered tips (Figure 2.1.21c–e) (Stewart, 1975). Tiwari and Wilkins (1995) reported that for at least the first 3 days of fiber development, the ultrastructure of fiber cells is typical of plant cells which enlarge by diffuse growth, rather than tip growth.

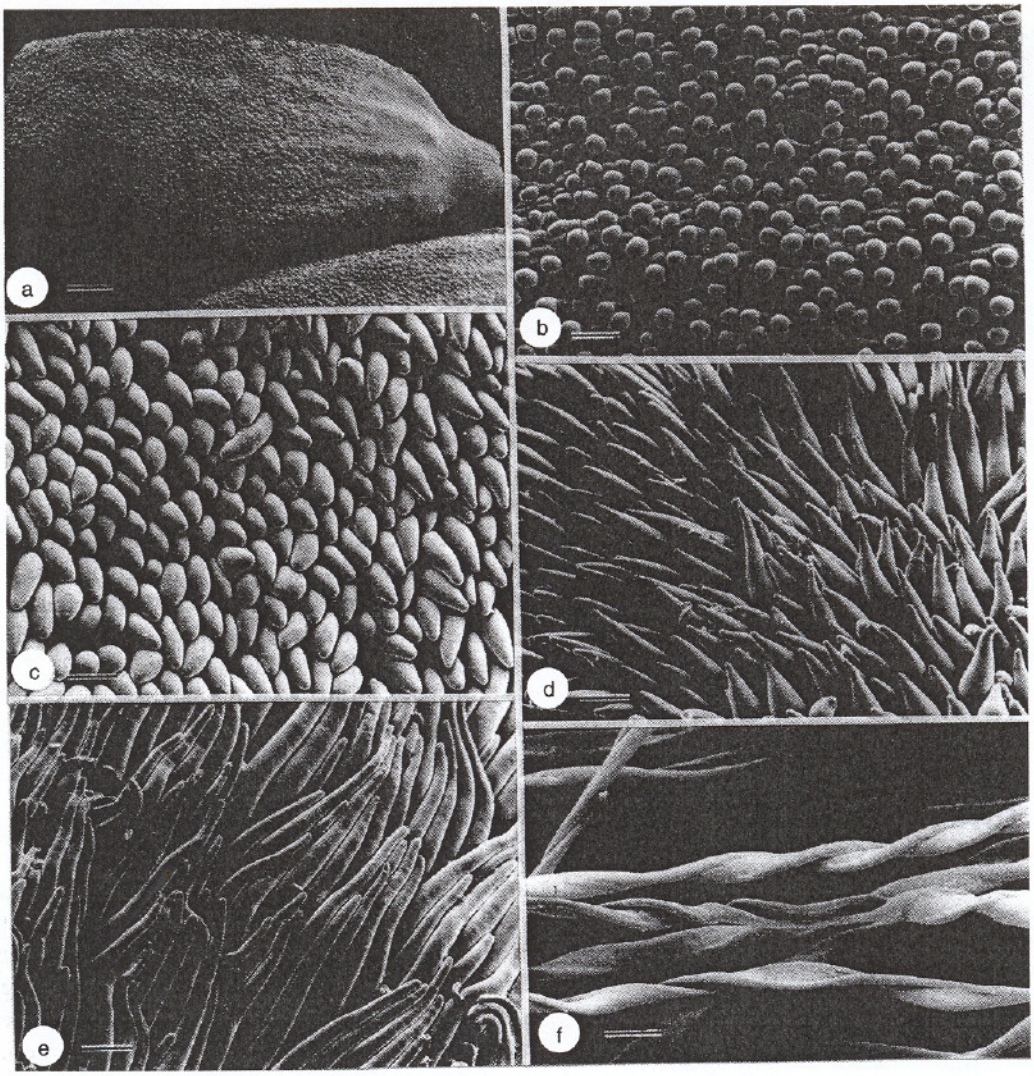


Figure 2.1.21. Fiber development. (*a*) Cotton ovule on the day of anthesis. (*b*) Fiber initials (primordia) on the day of anthesis. (*c*) Developing cotton fibers early on the day after anthesis (+1dpa). (*d*) Developing cotton fibers late on the day after anthesis (+1dpa). (*e*) Developing cotton fibers 3 days after white flower (+3dpa). (*f*) Mature cotton fibers (approximately +48 dpa). Scale bar = approximately 200 μm in (*a*), approximately 30 μm in (*b–f*).

Lint fiber elongation continues for about 20 days (Figures 2.1.17 and 2.1.21), eventually resulting in individual cells which range in length from 25 to 35 mm, depending on genotype and environment. The cell wall which is deposited during elongation growth is termed the primary cell wall, and it consists of pectin, callose, a thin layer of cellulose, and a cuticle on the surface (DeLanghe, 1986). Around 15–20 days after fiber initiation, deposition of the mainly cellulosic secondary cell wall begins. Thus in a population of fibers, as well as perhaps in individual fiber cells, elongation and secondary cell wall deposition overlap. Secondary cell wall deposition

continues until approximately 40–45 days post-anthesis, at which time the boll splits open. At this stage, the fibers dry, the central vacuole of the cell collapses, and the fibers assume a twisted ribbon-like shape (Figure 2.1.21f).

Embryo Development

The zygote divides 2–4 days after fertilization, and by about 7 days after fertilization the embryo has reached the globular stage. At this stage, certain regions of the globular embryo have been fated to form the cotyledons and the first and second foliage leaves (Christianson, 1986). By about 10–12 days, the two cotyledons are visible and the heart-shaped embryo is evident. This is followed at about 15 days post-fertilization by the so-called torpedo stage, with large cotyledons elevated straight above the forming shoot apex and procambium evident in the cotyledons and hypocotyl. From 15 to 20 days after fertilization, the cotyledons elongate greatly and become folded and coiled around each other. At this stage, the embryo is approximately 200–300 μm in length, and the shoot apical meristem and the root apical meristem are both completely differentiated. The first true leaf is produced by the young shoot apical meristem usually around 25–30 days following fertilization (Joshi et al., 1967). The endosperm resulting from double fertilization breaks down and is largely absorbed by the developing embryo beginning around 15 days after fertilization, until finally only remnants of the cellular endosperm persist.

FUTURE DIRECTIONS

To paraphrase Cutter (1978), contrary to the belief of many, we have not yet discovered all there is to know about the morphology and anatomy of the cotton plant or, for that matter, of any other plant species. In addition to basic understanding of the control of plant growth and differentiation, which is relevant to all of biology, our understanding of cotton management and production will benefit from further research into the developmental basis of structures and growth patterns that are unique to cotton. For example, our ability to produce columnar plants with the goal of decreasing unproductive fruiting positions will be enhanced by a more thorough understanding of the control of monopodial and sympodial branching. Similarly, understanding the spatial relationships of ovule protoderm cells destined to become fibers could potentially enhance our ability to manipulate fiber initiation and differentiation, key events that ultimately affect fiber quality and quantity. Future manipulation of leaf shape and position, root growth, source–sink relationships relative to maturing bolls, and many other aspects of the structure, development, and function of the cotton plant will require additional anatomical and morphological information. Finally, exciting insights into plant structure and development are coming from molecular biology and developmental genetics, usually as a result of studies with model experimental systems. The time is coming when these powerful approaches will be brought to bear on crop plants such as cotton, and the success of this research will depend in large part on a sound foundation in morphology, anatomy, embryology, physiology, and ecology.

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