Chapter 1

ANATOMY AND MORPHOLOGY OF FRUITING FORMS

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INTRODUCTION

As a woody perennial cotton has the most complex vegetative and reproductive morphology of any annual crop grown. Its growth habit produces both vegetative and reproductive organs simultaneously. The sympodial flowering pattern of the cotton plant causes a very complex production-distribution pattern of carbohydrate throughout the structure of the crop. Maximizing this production and distribution of energy is, of course, the goal of all growers' and research effort.

One of the earliest comprehensive descriptions of cotton plant morphology is that of J.M. Hector in ***INTRODUCTION TO THE BOTANY OF FIELD CROPS*** (1936) and the Russian monograph ***THE STRUCTURE AND DEVELOPMENT OF THE COTTON PLANT*** (Baranov and Maltzev, 1937). Mauney (1968, 1984, 1986) updated these descriptions based on anatomical details observed by Mauney and Ball (1959) which more accurately analyzed the association of the two branch buds found at the base of each leaf. More recently Oosterhuis and Jernstedt (1999) provided an overview of the morphology and anatomy of cotton No new observations which alter our understanding of the structure of the plant have developed over the decades since these earlier descriptions, therefore this review will use them to interpret several interesting features of highly productive modern cultivars.

VEGETATIVE GROWTH

The primary axis is the framework upon which the floral branches develop. This axis develops only roots, stems, and leaves. Because cotton is an indeterminate perennial, it continues to produce additional numbers of these organs until some stress such as drought, freezing, nutrient deficiency, terminates growth (Fig. 1).

The plant produces three types of leaves, cotyledons, prophylls, and true leaves. At the base of each leaf, a branch (axillary) bud primordium is left behind by the advancing apical meristem. This branch bud forms the axis for the axillary branches. The prophyll, the first inconspicuous leaf, resembling a stipule, is the first leaf to be formed by the branch axis. Since there is no internode formed below it, the prophyll resides in the axil where it was formed, though technically it is a part of the branch axis. In the axil of this prophyll an additional branch bud is formed to create what Mauney and Ball (1959) termed the “second axillary”. This bud is ordinarily dormant, but on very vigorous plants it may elongate and produce an additional branch axis (Fig. 2).

The representation depicted in Figure 2 is of a node from which vegetative branches (monopodia) develop. Morphologically these branches are indistinguishable from the primary axis.

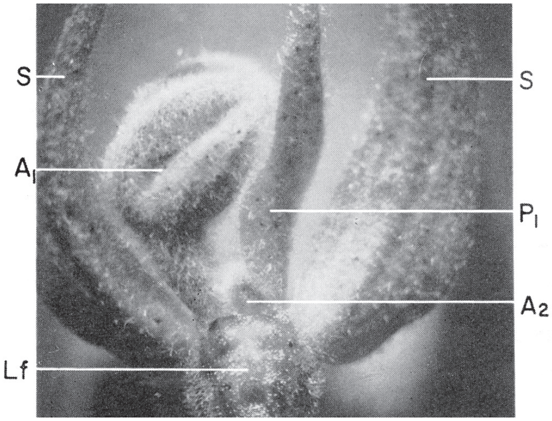

Figure 1. Young vegetative node of cotton. Lf = Leaf scar ; S = Stipules ; A_1 = First axillary; P_1 = Prophyll of first axillary; A_2 = Second axillary.

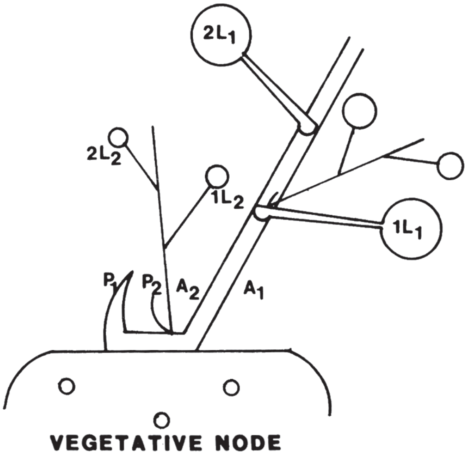

Figure 2. Schematic representation of a vegetative axillary branch . Sawtooths at left = prophylls; open circles = true leaves; P_1 = Prophyll of first axillary (A_1) ; P_2 = Prophyll of second axillary (A_2); 1, $2L_1$ = First and second leaf of first axillary; 1, $2L_2$ = First and second leaf of second axillary.

REPRODUCTIVE GROWTH

At some point early in the growth of the cotton seedling, the primary axis receives a signal from the leaves and begins developing nodes at which the first axillary shifts from vegetative branching to reproductive (sympodial) branching (Fig. 3). Morphologically these axes are identical to vegetative branches until the first true leaf is formed after which the meristem terminates in a flower. The branch continues by means of the axillary at the base of the prophyll of that true leaf breaking dormancy, elongating into a true leaf, and producing an additional flower.

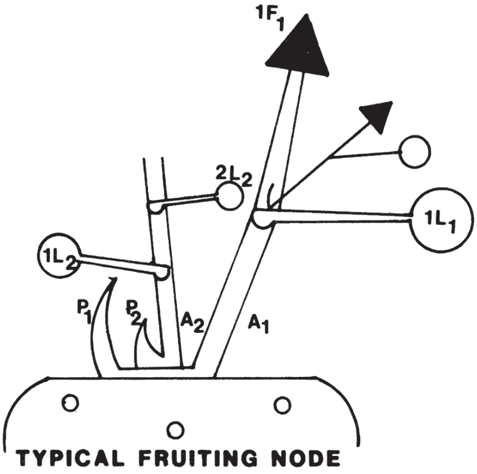

Figure 3. Schematic representation of a reproductive branch, sympodium. Black triangles = Flower buds, squares. $1F_1$ = First flower of first axillary. All other symbols are the same as Figure 2.

In robust plants with strong signals for flowering, the second axillary, which lies at the base of each branch, may also develop into a sympodium (Fig. 4). These fruiting structures often do not have a leaf opposite the flower, and as such do not have an axillary to continue the branch. Thus, they can appear as a single flower on a spur at any node on a fruiting branch. They are frequently functional flowers and contribute to productive yield. In certain heavy fruiting cultivars and open spacing situations the second axillary sympodia have true leaves, and may produce several flowers.

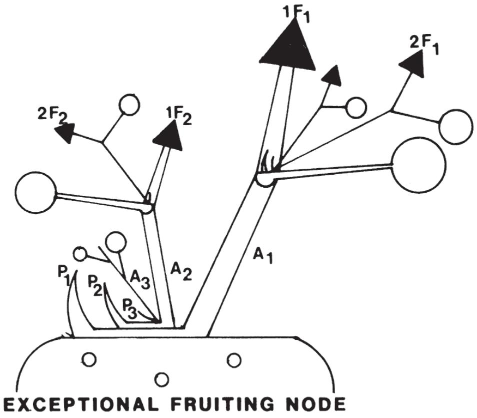

Figure 4. Schematic representation of a second axillary sympodium (A_2) and the resulting development of the third axillary (A_3). Other symbols are the same as Figures 2 and 3.

Since vegetative branches have the same potential as the primary axis, i.e., if they are vigorous, they will also bear sympodia. The signal to commence flowering seems to be received by all axes at the same time so that there are approximately the same number of nodes to the first flower on branches as on the main stem (Fig 5).

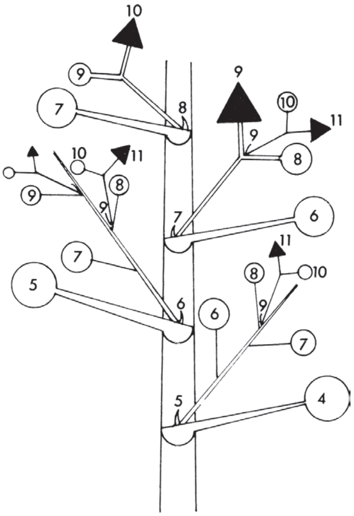

Figure 5. Schematic representation of square on sympoda on vegetative limbs and those of successive sympodia on the main stem. Numerals represent succession of leaf units (true leaves, prophylls, and bracts of squares). Other symbols are the same as Fig. 2 – 4. The plant represented had first flower at node 6. Though all leaf units are not precisely equal amounts of time, the events with equivalent leaf units should happen within a few days.

Flower Development

Reproductive branches are identical to vegetative branches throughout the development of the first true leaf. At that point the development diverges in that a whorl of three bracts occurs on the meristematic dome rather than the second true leaf of that axis (Fig. 4). These three bracts can be seen as a modification of the leaf and two stipules of vegetative development. The three bracts surround the meristem of the axis and terminate its vegetative elongation. Subsequently the floral meristem continues with whorls which become the calyx (fused sepals), corolla (sympetalus petals), androecium (with anthers), and gynoecium (pistil of 3-5 carpels with several ovules in each axil placentation) (Fig. 6).

The process of floral development from initiation to blossom takes about 40-45 days. At about the midway point of this process the leaf in which the branch develops begins to unfold and presents itself to sunlight. It is the top-most leaf of the vegetative axis and the flower bud (square) in its axil is at “pinhead” stage. About 21 days remain in the development of that flower before it opens as a white blossom and anthesis and pollination occurs (Fig. 7).

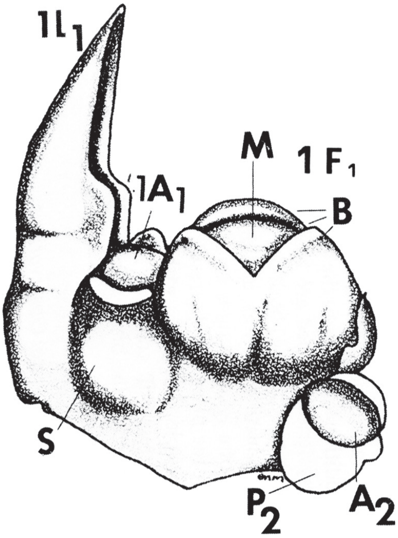

Figure 6. Artistic depiction of the orientation of the meristems which result in the formation of flower buds. The node depicted is about five nodes below the apex in the axil of a juvenile true leaf which has not yet expanded. At this point in the development of the branch, the three bracts (B) of the flower ($1F_1$) surround the dome of meristematic tissue which will form the petals and reproductive structures. The formation of the second axillary (A_2) and the second node of the sympodium ($2F_1$) can also be seen. Other symbols are the same as Fig.2-5. Drawing from Mauney (1984) by Edward Mulrean.

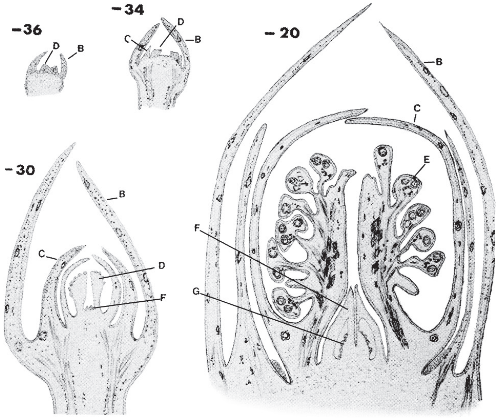

Figure 7. Development of a flower bud. Numbers refer to the estimated days prior to anthesis (Quintanilha *et al.* 1962). B = Bracts; C = Corolla; D = androecium; E = anthers; F = Ovary (locules); G = Ovules. Drawing adapted from Baranov and Maltzev, 1937.

Environment is influential throughout the development of the floral organs. The signal to initiate production of sympodia can be enhanced or delayed by excessively high or low temperatures (Mauney, 1966). Meiosis resulting in pollen and ovule initiation takes place about 20-22 days before anthesis (DBA) (Stewart, 1986). This process is temperature sensitive, so that at high temperatures sterile pollen may result (Meyer, 1969; Fisher, 1975). It is also affected by certain herbicides (including Glyphosate) if applied during this time frame (Yasour, *et al.*, 2006).

On the day the flower matures and opens (anthesis), the anthers dehisce, pollen is deposited on the stigma, it germinates, and pollen tube growth begins. Pollen tube growth is sensitive to high temperatures (Snider, *et al.* 2011) which may result in poor fertilization and reduced seed number. Fertilization of the egg and endosperm occurs about 12 to 30 hours after anthesis (Stewart, 1986). Embryo growth begins about 4 to 5 days after anthesis (Quintanilha, *et al.* 1962).

The embryo sac expands rapidly after anthesis driven by the expanding endosperm. The ovule and developing boll reaches 90% of mature volume about 20 days post anthesis (DPA).

Growth of the embryo lags behind that of the ovule and endosperm, but follows a sigmoid growth pattern (Fig 8). In early growth the embryo is nourished by the endosperm, which becomes cellular and is absorbed by the cotyledons as they mature. At about 24 DPA the boll reaches mature volume, and the cotyledons fill the ovule. (Leffler, 1976) Mature boll weight occurs at about 35 DPA, though environmental stresses may delay boll opening for several weeks.

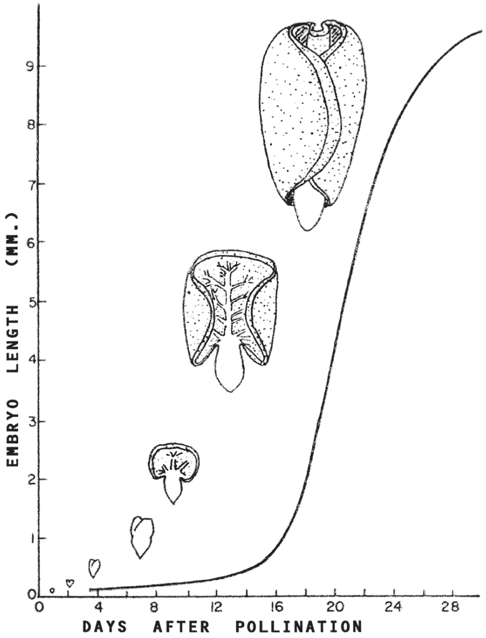

Figure 8. Growth of the cotton embryo. Sigmoidal curve is a plot of length of the embryo against age from pollination. Illustration shows degree of differentiation at various stages of development.

Vascular Connections of the Boll

The developing cotton fruit receives water and nutrients from subtending leaves and the rest of the plant in an elaborate manner related to the vascular network of the stem and connections of individual bolls. Brown (1968) used ^{14}C-labelled sucrose to show that leaf assimilate moved in well-defined strands of phloem related to the 3/8 phyllotaxy of the plant. He found the pattern of translocation down the plant occurred mainly to sympodia which arose on the same side of the main axis.

The developing boll receives its water mainly from the phloem and not the xylem (Van Iersel, *et al.* 1994). They presented evidence that xylem vessel to bolls to not mature until after the three-week period of rapid increase in boll size. No significant apoplastic water moved into developing bolls during the first three weeks after anthesis indicating that that xylem was not the main source of water for the expansion of the young fruits. These authors (Van Iersel, *et al.* 1995) also used specific phloem tracers to show that phloem was functional in the capsule wall and central column of the boll from the early stages of development. Phloem was the major source of water for the developing bolls. The isolation of the apoplast from the rest of the plant explained why cotton fruits had higher water potential than subtending leaves (Trolinger, *et al.*, 1993) and were less sensitive to drought (Van Iersel and Oosterhuis, 1996).

Fiber development has been described in an excellent article by Delanghe (1986). In summary, fiber elongation begins in certain epidermal cells of the ovule on 1 DPA. Elongation continues for about 20 DPA during which stresses have an effect on fiber length. At 16 DPA secondary thickening begins and environmental factors affect fiber strength and maturity.

Four Bract Squares

Certain environmental conditions cause the plant to produce four-bract squares instead of the common three-bract flower bud. If we interpret the typical 3-bract square as a modified leaf and two stipules, then it is easy to interpret the fourth bract as a modification of the second leaf on the branch. What happens is that in conditions where the plant is in transition from vegetative to flowering the meristematic dome on which the three bracts arises is not consumed by those bracts and continues its activity as if were making the next node on a vegetative branch. This modified leaf becomes the fourth bract (Fig 9). In extreme cases that modified leaf (bract) may have modified stipules and the flower bud may have five or six bracts.

Figure 9. Photograph of three and four bract squares. The square on right is typical three-bract square. The square on left has four well form bracts. The fourth bract (arrow) on the square in the center is not well formed and the air gap produced as it expands can allow thrips to enter and feed on the unprotected androecium (20 DPA Fig.7).

Morphologically these extra bracts do not cause abnormalities in fruit development, but they do present an opportunity for insect damage. Because the fourth bract is usually not well formed, it does not seal tightly against the other bracts, and structural gaps appear as the bud matures. These gaps afford an opportunity for thrips (which are always present) to enter the square while the petals are not yet protecting the developing ovary and androecium. Feeding of thrips on these structures will cause the square to abort (Mauney and Henneberry, 1984).

The well formed thicket of young leaves, internodes, and developing squares that comprise the apical growing point above the youngest expanding leaf of the healthy plant is too tightly matted to be invaded by casual feeders such as thrips. At the point when the leaf of a given node begins to unfold and expand, the square in its axil is approximately three weeks before anthesis (20 DBA, Fig 7). At this stage the petals have not yet expanded sufficiently to envelope the ovary and androecium. The interlocking serrations of the bracts ordinarily prevent thrips from these tissues. However, the fourth bract does not interlock with the others, allowing thrips to introduce bacteria which trigger a soft rot, causing the square to abort.

Reversion to Vegetative Growth

Early fruiting cultivars are sometimes subjected to excessive temperature and humidity after they have set the first fruiting branch. These extreme conditions can lead to production of vegetative branches after the development of sympodial branches has commenced. It is no longer rare to have vegetative branches develop at nodes above the lowest sympodia. In the monsoon climates of India and Pakistan this reversion has always been a concern and limited the season on some cultivars.

Morphologically this phenomenon demonstrates that each axillary primordium receives its own signals for development, and that high temperature is a negative signal for floral development (Mauney, 1966). Fortunately for the productive season these vegetative branches remain relatively rare in the canopy. Development of sterile pollen, discussed above, is also an affect of high temperature-humidity, and is more likely to affect productivity than location of vegetative branches.

Cutout

Vegetative elongation and production of additional nodes by the plant apex is more sensitive to internal and external stresses than is the development of floral buds into flowers. Thus, once flowering commences the progression of the flowers up the stem is usually faster than the addition of new flowering nodes. That is, the rate of flower movement up the stem begins at a rate of about three days per node (0.33 nodes/day) and declines to about four days per node (0.25 nodes/day) as the season progresses, whereas the rate of new node production begins at three days per leaf and declines to ten days per leaf as the season progresses (Fig. 10).

The disparity between these rates means that at some point in the season the plant will run out of sympodia and must pause in the flowering process until the carbohydrate stress produced by boll maturation is relaxed and vegetative elongation of the apex can resume. This process is known as “cutout” and is always seen in a well fruited cotton planting. In locations with a very long productive season, the crop may have time to produce additional productive nodes from this regrowth and thus resume the fruiting cycle after cutout.

The slope of the intersecting trend lines in Figure 10 determines the timing of cutout for any particular cultivar and season. Ordinarily 10 to 15 fruiting nodes are produced by each plant in any 150-day productive season. The trend lines are influenced by the timing of floral initiation, the tendency of the cultivar to partition nutrients to fruit versus vegetative structures, particularly roots, and seasonal stresses (Landivar *et al.*, 2010; Mauney *et al.*, 1978; Patterson *et al.*, 1978).

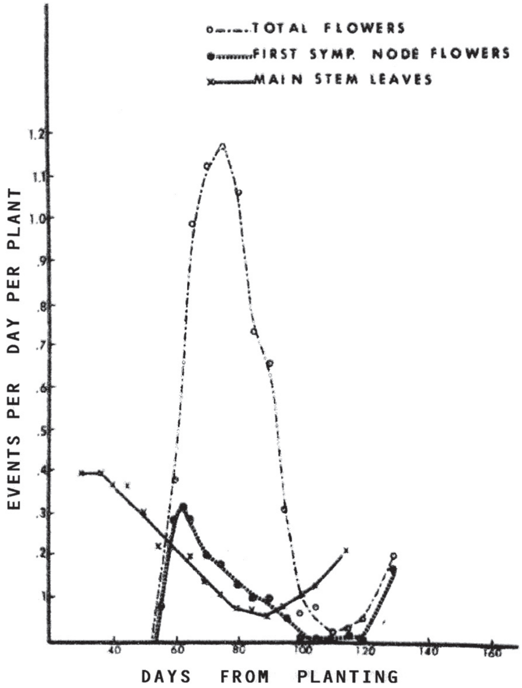

Figure 10. Relationship of production of new flower positions represented by new leaf formation and flowering rate from those positions. “Events per day” is the inverse of “Days between events”.

Several crop monitoring programs have been devised to predict the timing of cutout (Kerby, *et al.* 2010, Landivar, *et al.* 2010, Oosterhuis and Bourland, 2008). These programs use the number of main-stem nodes above the uppermost first-position flower (NAWF) as a measure of the approach of cutout. Though in intensively managed plantings, such as those with sub-surface drip irrigation and fertilization, it has been observed that harvestable bolls can be set from flowers very close to the terminal (Mauney, personal observation), it has been usually found that when NAWF is five or less cutout has occurred. That is, few harvestable bolls will be set until the planting has resumed vegetative growth with the production of additional sympodia.

CONCLUSIONS

As a perennial shrub the cotton plant is unique among annual crops in the USA. Because each of the fruiting structures depicted in Figure 5 has an individual time line of development with points of sensitivity to internal and external stresses which differ from all the neighboring fruiting forms, the analysis of effects of stress may be complex indeed. Thus, stress at any time in the entire 150 to 200 days between planting and harvest will affect some developing fruit.

Beginning with the transition from production of vegetative branches to sympodial flowering structures the plant demonstrates sensitivity to environment at every stage. The number of bracts in the flower, the viability and growth of pollen, the distribution of nutrients to the bolls, and the continued production of fruiting sites through vegetative growth are all dependent on favorable temperature and moisture conditions.

By the same token the crop has a remarkable ability to “compensate” for stress by maturing fruit before or after the stress. The marvel is that the crop is so resilient and production and is rather predictable.

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