

Chapter 22

CARBOHYDRATE DISTRIBUTION IN BOLLS

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INTRODUCTION

Assimilate distribution in the cotton plant depends on several factors: (1) carbon dioxide exchange rates (CER) of leaves and other photosynthetic tissues; (2) relative strengths of bolls and other sinks; (3) source-to-fruit proximity and other translocation factors; and (4) duration of transport into fruit.

ASSIMILATE SUPPLY

Pinkhasov (1981) summarized years of research on cotton photosynthesis and assimilate distribution, in which total plant photosynthesis was divided among contributing organs. Main stem leaves contributed 33 percent of the photosynthesis; lateral branch leaves, 55 percent; bracts, 4 percent; fruiting organs, 2.1 percent; petioles, 4.4 percent; and cortex, 1.5 percent. The higher CER of lateral branch leaves over main stem leaves was attributed to the higher rates of assimilate export from the lateral branch leaves. (More will be said later about the relationship of CER and translocation rates.) Pinkhasov found that CER/unit of plant weight peaked at budding time (approximately 45 days after emergence under his growing conditions) and then declined. This peak period was thought to be due to favorable temperatures and a low level of mutual shading. CER/plant and leaf area peaked during the fruiting period (approximately 100 days) and

then declined as crop maturation progressed.

There is general agreement in the literature that leaves, bracts and other structures supply assimilate to the developing boll. Using autoradiography, Brown (1968) found that bracts, carpel walls, subtending leaves and other leaves higher on the main stem supply assimilate to the boll. From more quantitative work, Ashley (1972) and Benedict and Kohel (1975) agree that the subtending leaf is the major source of assimilates for its associated boll. When fruiting branches were allowed to assimilate $^{14}\text{CO}_2$ following removal of leaves, bracts or both, Benedict and Kohel (1975) found that the associated bracts supplied only 5-10 percent and the carpel wall contributed very little of the developing boll's assimilate. The importance of the subtending leaf is confirmed by the parallel time courses of assimilate efflux from the source leaf and influx into the seed, both of which peaked at 6 hours following incorporation of the label. Ashley (1972) observed a similar time course for efflux with the fastest rates between 2 and 8 hours. Ashley also showed that more than 89 percent of the assimilate fixed in a source leaf remained in that sympodium throughout the 24-hour observation period. This is consistent with the relative importance of main stem and lateral branch leaves observed by Pinkhasov (1981), who reported the assimilate tends to be used by sinks near the source. Elmore and McMichael (1975) found that photosynthesis was equal in normal and nectariless bracts but was reduced to 64 percent of the normal in cotton with frego bracts. This would not be a serious problem in frego bract lines, since the contribution by bracts is small.

Photosynthesis has been reported to limit cotton productivity. Hesketh *et al.* (1972) reported that CO_2 enrichment doubled the number of bolls per plant. Guinn *et al.* (1976) reported that increasing atmospheric CO_2 content from 330 ppm to 630 ppm caused an immediate 65 percent increase in CER which declined to a steady 31 percent increase in CER. The CO_2 -enriched plants had more blooms and a lower boll abscission rate resulting in more bolls. Enriched plants also used more nitrate. There was a 65 percent increase in boll weight. In subsequent work, Mauney *et al.* (1978) showed that CO_2 enrichment was accompanied by a 15 percent increase in CER and increases in leaf area, boll set and boll weight. Growth analyses showed that the additional assimilate in the high CO_2 treatments was partitioned first to higher leaf area and plant dry weight in young plants and later to additional bolls. The combination of high CO_2 and additional mineral nutrients to meet the demands of the increased growth produced a 180 percent increase in harvestable lint weight. When extrapolated to land area, these yields were equivalent to 3,250 kg/ha (5.8 bales/ac). Mauney *et al.* (1978) concluded that, if reliable measurement methods could be developed, increasing CER would probably be an important means of increasing cotton yields. Since leaf area and plant dry weight in juvenile plants responded to increased CO_2 , these variables might be useful screening tools. Wardlaw (1980) wrote that in:

some crop species, yield increases were due to improved harvest index rather than to increased biomass or photosynthesis. Gifford and Evans (1981) concluded that most yield increases have resulted from increased harvest index. Improved CER may increase yields of economically important plant parts or products, but not necessarily. This depends on how the photosynthate is partitioned among plant parts.

Photosynthetic and translocation processes interact in cotton and other plants. When photosynthesis is very low, the quantity of assimilate available for translocation is reduced. McArthur *et al.* (1975) reported that when cotton plants were kept in darkness for 48 hours, they shed most of their flowers and young bolls 2 to 3 days after the dark treatment. They concluded that only a 1 or 2-day supply of sugar and starch was stored in the leaves and that assimilate translocation ceased after that time. They theorized that shedding was a means of maintaining a fairly constant carbohydrate level in the plant. There is also an effect of translocation on photosynthesis, because assimilate accumulation in leaves appears to inhibit photosynthesis. Through this mechanism, sinks (plant tissues or organs which are net importers of assimilate) can exert some control over assimilate production (Gifford and Evans, 1981).

Pinkhasov (1981) reported that, when all fruiting organs were removed from cotton plants, CER decreased 3-fold and assimilate efflux from leaves decreased. Mauney *et al.* (1979) cited reports of self-limiting behavior of photosynthesis. These involved a reduction of CER at times during the day when conditions were favorable for photosynthesis. Hypothetically, this reduction could have been caused by stomatal closure due to "localized water stress," hormonal changes or accumulation of photosynthetic products. Ackerson and Hebert (1981) and Ackerson (1981) have shown that leaf carbohydrate does increase during water stress cycles. This reaction caused a reduction in photosynthesis unrelated to stomatal factors in stress-adapted leaves compared to non-adapted leaves when water status was adequate. These adapted leaves had higher CER than non-adapted leaves during periods of water stress. Under adequate moisture, chloroplasts in adapted leaves had unusually large starch grains and appeared swollen with some thylakoid membrane breakage.

In early reports, Mauney *et al.* (1976) found that a 100 to 250 mg g⁻¹ increase in leaf starch content was accompanied by a decrease in CER from 40 to 30 mg CO₂ dm⁻² hr⁻¹. Mauney *et al.* (1979) found that there were no significant correlations between leaf sugar content and CER in greenhouse-grown cotton. They did report significant negative correlations between starch content and CER in cotton grown at normal CO₂ levels (330 ppm) in the greenhouse. An increase of leaf starch content from 40 to 150 mg g⁻¹ reduced CER by about 10 percent in cotton. This range in starch content was observed both in the greenhouse at normal CO₂ levels and in the field. Field-grown cotton and cotton grown at 630 ppm CO₂ did

not, however, exhibit a significant correlation of CER and starch content. The authors point out that since photosynthesis produces starch, a positive correlation of CER and starch would be expected even if starch were inhibiting CER slightly at certain starch levels. The "cause-and-effect relationship tends to mask inhibition of photosynthesis by starch" (Mauney *et al.*, 1979). They observed no negative carbohydrate-CER correlations in sunflower, soybean or sorghum. Although there was no significant correlation of starch and CER among cotton leaves in 630 ppm CO₂, there were diurnal increases in starch and decreases in CER during each of the first three days after cotton plants were transferred from normal to high CO₂ greenhouses. When cotton was transferred from high CO₂ to low CO₂, CER increased to normal levels as midday starch content decreased from 235.5 to 145 mg g⁻¹. Mauney *et al.* (1979) concluded that although high CO₂ overshadowed the inhibitory effects of high leaf starch concentrations on CER due to high substrate level, it is reasonable to conclude that inhibition was occurring in the greenhouse at high CO₂ contents and in the field. C.W. Chang (1979) found that starch contents become high enough to restrict photosynthesis in young leaves (the top four leaves), but not in older leaves.

SINK STRENGTH

Sink strength is important in determining how a plant distributes its assimilate among plant parts. As previously stated, harvest index is important in determining yields of specific plant products or structures, such as cotton lint or seed, which are of economic value. In this chapter, sink strength is defined as the ability of an organ, e.g. a cotton boll, to import assimilate for its use. In theory, the use might be for development of economically important products or for economically insignificant metabolic activity or excessive vegetative growth. Since we are interested in efficient seed cotton production, we must also be interested in efficient assimilate conversion into lint and seed. Of course, the plant must have sufficient root, stem and leaf growth to support boll growth, but we are primarily interested in understanding the sink strength of developing bolls.

Hesketh *et al.* (1976) studied basic growth relationships in cotton to determine what constitutes an efficient plant. They concluded that there is probably a point beyond which increasing harvest index would be counter-productive. A minimum vegetative framework is undoubtedly required for dependable plant survival. They found that as leaf area increased, total stem weight, stem weight per unit length, and total plant size increased. Pinkhasov (1981) reported that most labeled assimilate went to leaves and stem until the beginning of flowering. As fruit development progressed toward boll maturity, more and more assimilate went to the bolls. Munro (1971) reported that the first three positions on the sympodium accounted for the majority of mature bolls and received the majority

of assimilate partitioned to reproductive growth. Ashley (1972) found that bolls close to photosynthetically active leaves are strong sinks. This does not, however, preclude the shedding of very young bolls which are closer to the source leaf but are weaker sinks than a larger, actively growing boll nearby. Assimilate may also be imported from more distant sources when the leaf subtending that actively growing boll can no longer meet its assimilate demands because of shading (McArthur *et al.*, 1975). Pinkhasov (1981) reported the same trends, indicating that a leaf on a sympodium sent most of its assimilate to the closest boll if that boll was 16 to 35 days old. He found the peak influx period to be 20 to 27 days, when the boll drew assimilate from distant as well as the closest leaves preferentially over younger bolls. He attributed the loss of 80 to 85 percent of fruiting organs to this competition for assimilate. Pinkhasov described this fruit loss as a survival mechanism, because the early bolls which are more likely to reach maturity are most competitive for assimilate.

Hesketh *et al.* (1976) concluded that production of late season flowers whose bolls will not mature may seem wasteful, but the increased fruiting branch leaves which accompany flowering may be important in crop maturation, since cotton leaves often senesce rapidly. If "wasteful" flower production were eliminated, extending leaf activity or breeding for more leaf production might be necessary.

Sink strength can be defined in a variety of ways depending on the plant species. In wheat, sink strength has been characterized by dry weight increase $\text{ear}^{-1} \text{hr}^{-1}$ (Wardlaw and Moncur, 1976) and was positively related to rate of assimilate transport through the peduncle. Cook and Evans (1978) correlated sink strength to the number of developing grains per wheat head. The large sinks imported more assimilate than did heads from which grains were removed after anthesis. There was a complication in their findings in that the small sinks imported more assimilate per grain than did the large sinks, especially from reserves. Boote (1975) found that dry weight of peanut fruit was proportional to sink strength. Snyder and Carlson (1978) reported that translocation of assimilate was directly proportional to the taproot-leaf weight ratio in sugarbeet.

While sink strength is often correlated with the physical size or weight of the sink, it is important to realize that sink strength is a function of metabolic demand. Certain portions of metabolic demand, such as respiration, may be a function of tissue mass. Other portions may be related to specific synthetic activities occurring in the sink during a particular developmental period which are not reflected in mass or size of the sink. Benedict *et al.* (1980) reported this to be the case with cotton. Data for boll size plotted against boll age (the number of days after anthesis, DPA) resulted in a hyperbolic pattern. The data were fitted to a fifth degree polynomial equation which resulted in an accumulative curve for the fresh weight of the boll (correlation coefficient 0.913) (Figure 1). The derivative of the polynomial resulted in a rate curve of boll size with the maximum

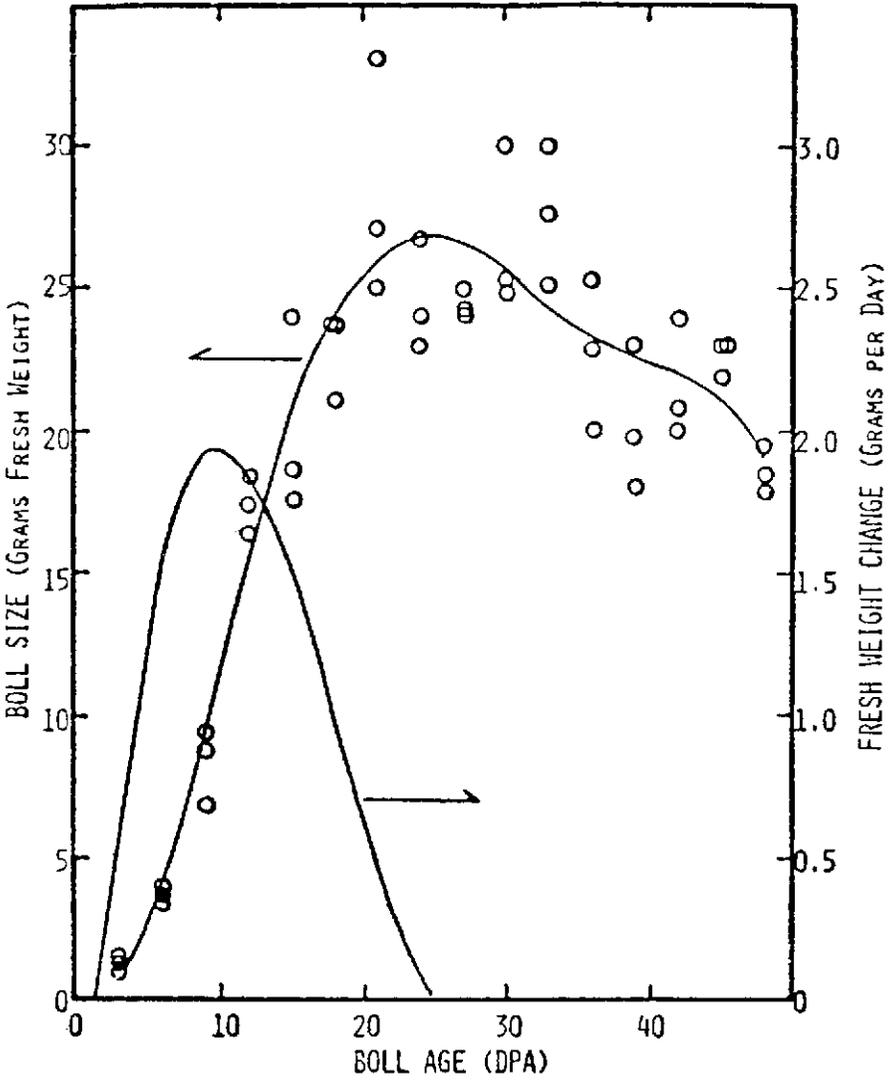


Figure 1. The best-fit curve for the increase in the boll size of different age bolls and the derivative of this curve resulting in the rate curve of boll size.

increase of boll size at 10 days past anthesis (DPA). Increase in boll size stopped 25 DPA. When the distribution of ^{14}C -assimilates, from a 20 hour translocation period, into different age cotton bolls was examined, there was only a small amount of ^{14}C -assimilate transported to 10 day old bolls (Figure 2). The amount of ^{14}C -assimilate transported to cotton bolls reached a maximum 31 to 32 DPA, then the amount transported declined to zero at 45 DPA. The curve for the partitioning of ^{14}C -assimilates to different age cotton bolls does not correlate to the rate curve describing the increase in boll size. An increase in the size of cotton bolls to 25 DPA is primarily due to an increase in the fresh weight of the carpel wall. Benedict *et al.* (1973) have previously established the curve describing the partitioning of ^{14}C -assimilates into carpel walls of different age cotton bolls which is similar to the curve for increase in boll size. Baranov and Maltzev (1937) have shown that even though the size of cotton bolls reach a maximum 22 to 25 DPA, the embryo does not reach maturity until much later (See Chapter 20).

Schubert *et al.* (1973) have shown that the rate of fiber weight increase of Stoneville 213 cotton reaches a maximum 30 to 31 DPA and then declines to zero at 55 DPA. Similar patterns were observed in Pima cotton (Schubert *et al.*, 1976). Thus, the partitioning of ^{14}C -assimilates to different age cotton bolls reflects the distribution of ^{14}C -assimilates to ovular constituents and lint fibers rather than the distribution of assimilate to carpel wall. Benedict *et al.* (1980) reported a good correlation of the distribution of assimilates to different age cotton bolls and their lint fibers (Figure 3). Curves describing the partitioning of ^{14}C -assimilate to lint fibers and the rate of weight gain in lint fibers during boll development were also similar with a correlation coefficient of 0.876 for points on the two curves. The distribution of assimilates to different age cotton fibers is highly correlated to the cellulose deposition or sink demand of the different age fibers (Figure 4). This relationship was strengthened by a comparison of the partitioning of ^{14}C -assimilates to lint fibers and the rate of cellulose synthesis in excised ovules (Figure 5), as indicated by the rate of ^{14}C -glucose incorporation into cellulose of different age lint fibers. Again, the time courses of assimilate partitioning to lint fibers and cellulose deposition were almost identical. The overall assimilate influx pattern (and, therefore, sink strength) of developing cotton bolls reflects the time-course of their dominate metabolic activity—synthesis of cellulose in the lint fibers—rather than just boll size (Benedict *et al.*, 1980).

SOURCE-TO-SINK PROXIMITY

The proximity of sinks to sources of assimilate is an important factor in the distribution of assimilate. Tuichibaev and Kruzhilin (1965) reported that labeled assimilate from leaves near the bottom of the plant moved primarily to the roots in

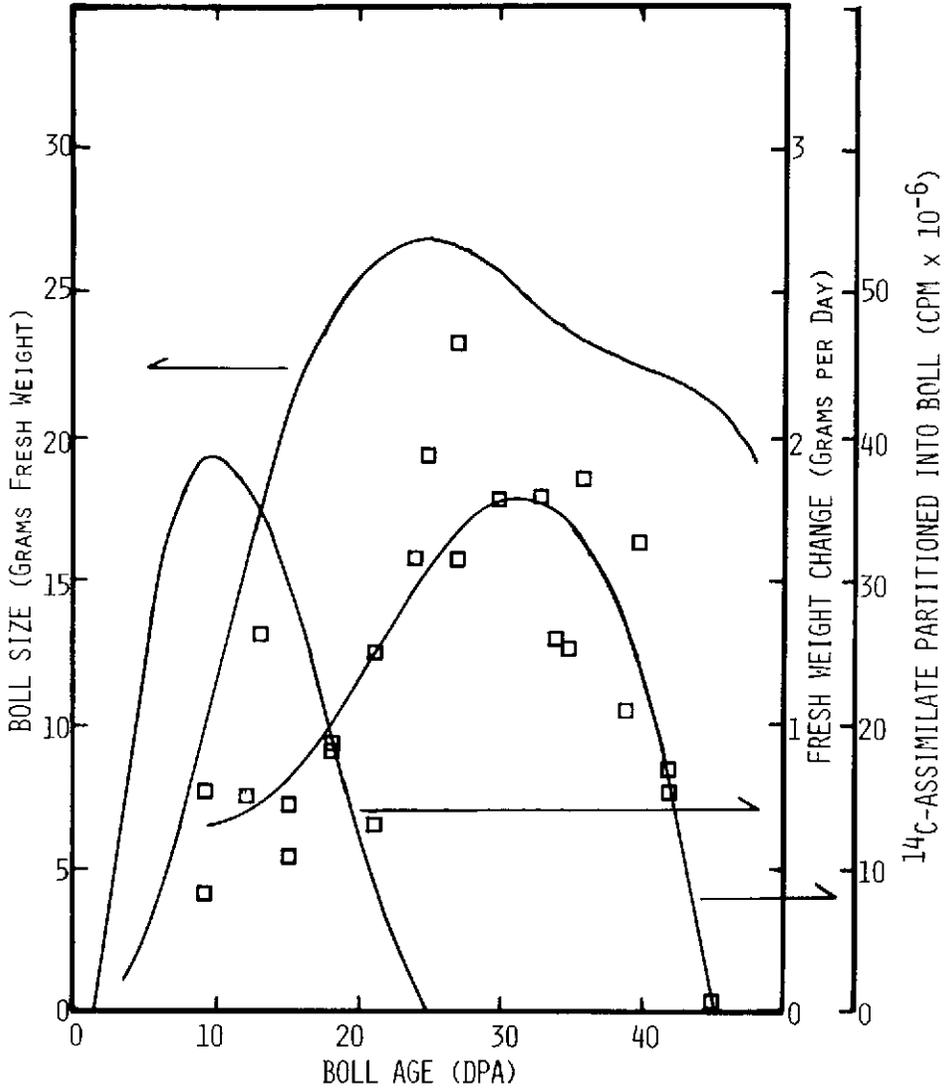


Figure 2. The best-fit curve of the partitioning of ¹⁴C- assimilates into different age cotton bolls versus the best-fit curve for boll size of different age cotton bolls and the differential curve describing the rate of increase of boll size in different age bolls.

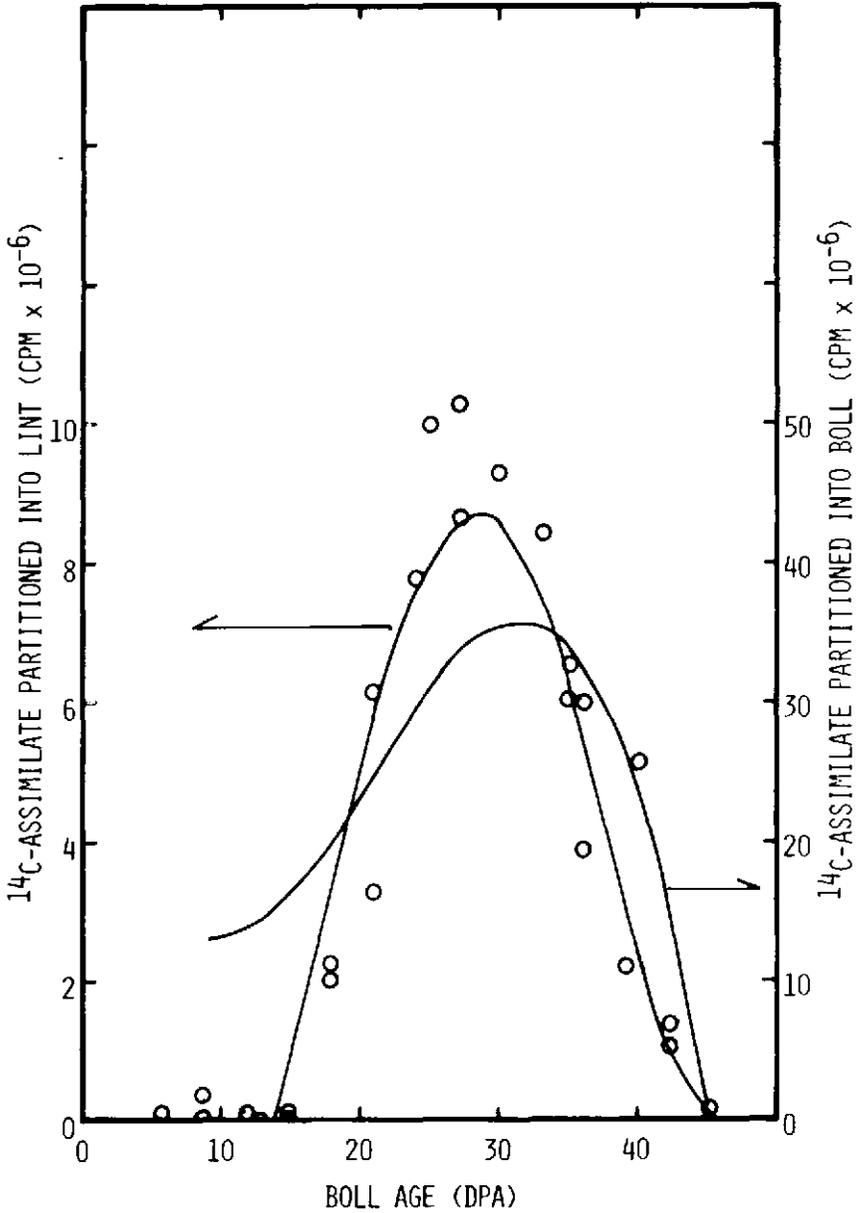


Figure 3. The best-fit curves for the partitioning of ^{14}C - assimilates into different age cotton bolls and the partitioning of ^{14}C - assimilates into cotton lint fibers in different age cotton bolls.

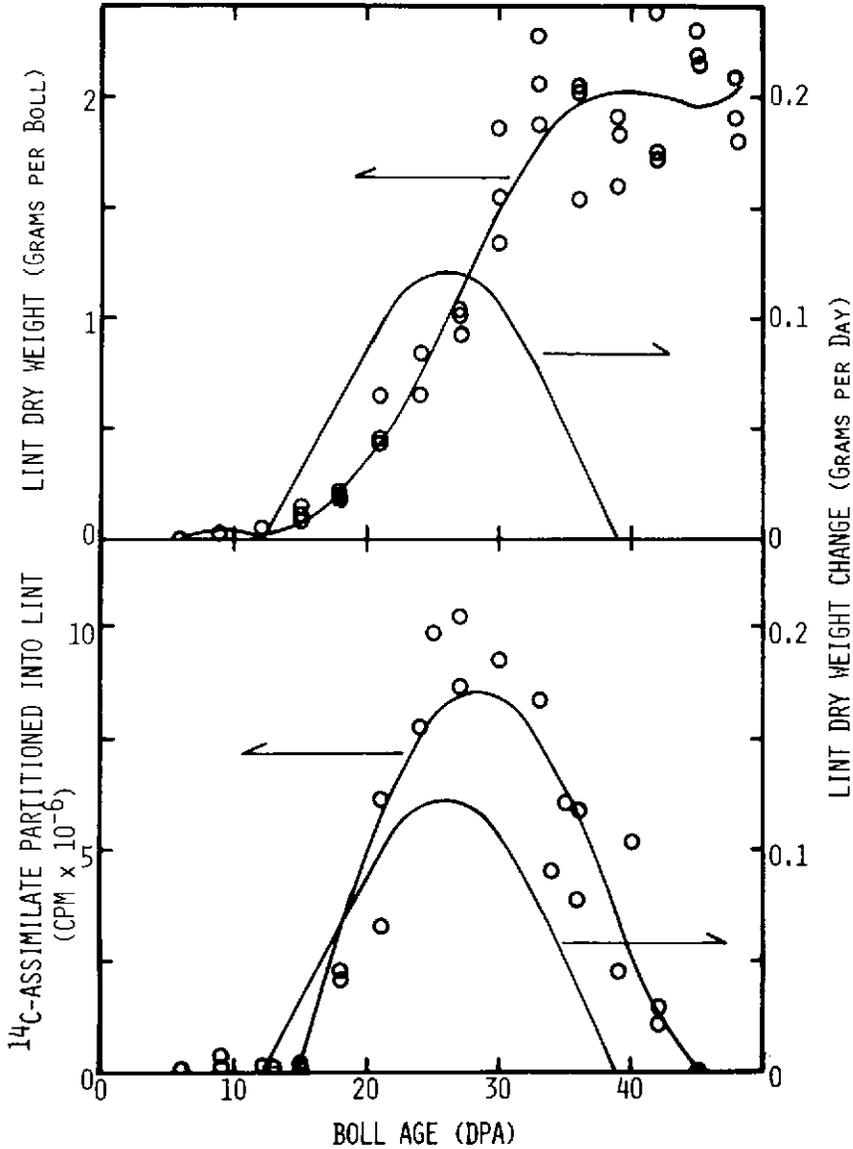


Figure 4. Upper part, is the best-fit curve describing the accumulative increase in dry wt of different age cotton fibers and the differential of this S-shaped curve to give the curve describing the rate of dry wt increase (rate of carbon deposition) in different age fibers. Lower part, the curves for partitioning the ¹⁴C-assimilates into different age cotton fibers and the rate of dry wt increase in different age fibers.

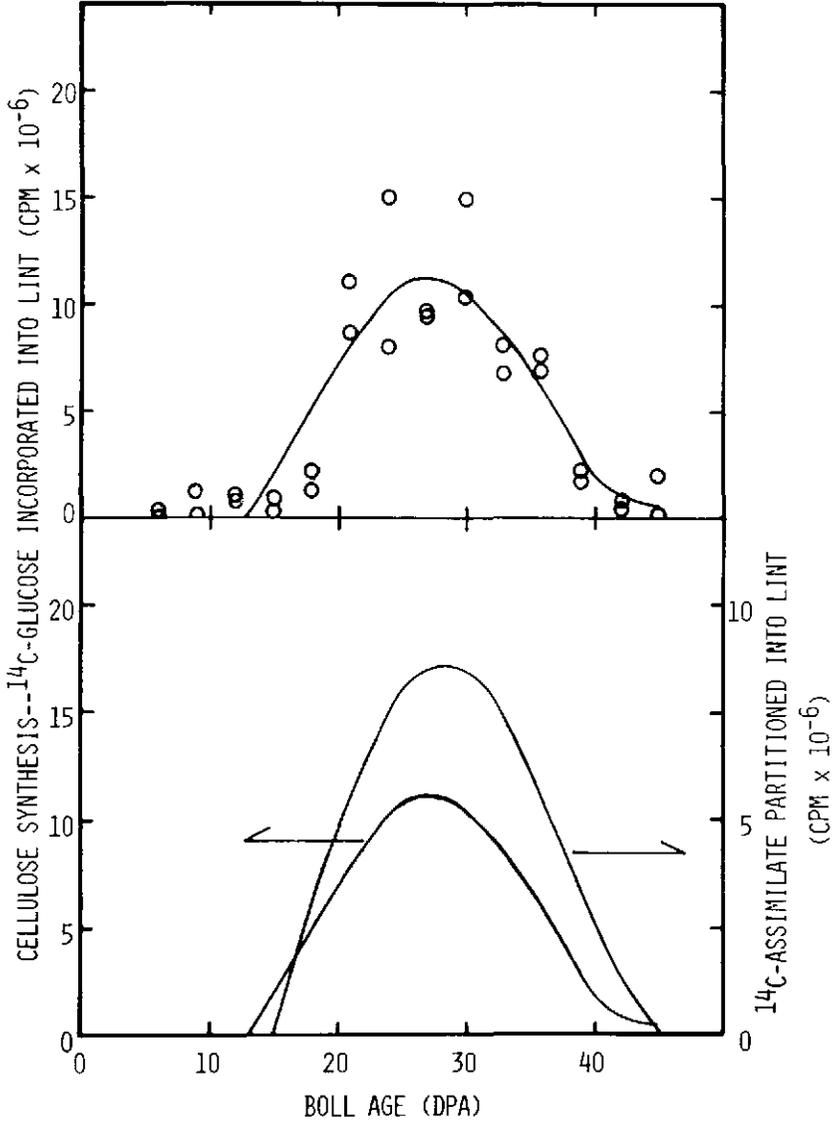


Figure 5. Best-fit curve for the rate of cellulose synthesis in excised ovules (upper part). Curves for the partitioning of ¹⁴C-assimilates into different age fibers and the rate of cellulose synthesis in excised ovules (lower part).

young, vegetative cotton plants. Progressively less labeled assimilate moved to the roots from successively higher leaves. As was previously discussed, Ashley (1972) reported that actively growing cotton bolls were strong sinks for assimilate from nearby leaves.

Pinkhasov (1981) reported on experiments with a cotton cultivar which had an average distance of 24 cm from source leaf to fruit and a mutant with only 14.8 cm distance. Both genotypes had similar whole plant CER. The rate of efflux from the source leaf was twice as fast for the mutant as for the normal cultivar, as was the influx rate into the boll. The mutant had a much lower influx of labeled assimilate into the stem and root. The normal line had a leaf weight:fiber weight ratio of 1:1.99; the mutant had 1:3.49. A Duplex cultivar which has shortened sympodial branches with double bolls, small leaves and a leaf to boll distance 1.5 times shorter than normal lines also exhibited higher yields and earlier maturity than normal cultivars. Pinkhasov theorized that, since translocation is an energy-requiring process, energy is conserved when the translocation distance is shortened. There is also a reduction in the assimilate used to produce and maintain stem tissue. The shorter source-to-sink lines were more productive than normal cotton in the field when plant population was increased.

Other factors also affect translocation rates and assimilate partitioning. Ashley and Goodson (1972) reported that potassium deficiency reduced translocation velocity in cotton from 50 to 20 cm hr⁻¹.

Some assimilate may be tied up in storage pools which are not readily available for later use. Chang (1980) studied the relationship of leaf sugar and starch contents, starch degradation in darkness, and amylose and amylopectin dynamics during development in cotton. He found that starch degradation was not accompanied by an increase in leaf sugar content unless the phloem was disrupted by girdling, indicating that sugar released from the starch pool was immediately translocated. Sugar translocation was equal to or faster than starch degradation. The sugar increase after girdling also indicated that sugars produced by starch degradation were not broken down in the leaves to any great extent. Until about 50 days after planting, 70 to 80 percent of the starch in young leaves broke down during a 14-hour dark period, but only 30 percent in old leaves. After 62 days, there was a preponderance of older leaves, starch levels were not as high during the light period, and young and older leaves were more similar in starch degradation percentages in the dark. Chang reported that the main difference in starch degradation was due to changes in the ability of different aged leaves to break-down amylose and amylopectin. As leaves aged, amylopectin degradation decreased. Since amylopectin made up 75 to 90 percent of leaf starch, remobilization decreased greatly in older leaves and older plants which had a preponderance of older leaves.

Thompson *et al.* (1975) reported that levels of both soluble and insoluble

carbohydrates increased in leaves during unseasonably cool temperatures, apparently due to inhibition of translocation and growth.

DURATION OF ASSIMILATE TRANSPORT TO BOLLS

One of the classical factors determining crop yields is the length of the fruit filling period, along with number of fruit and assimilate partitioning to the fruit. In examining these factors, Duncan *et al.* (1978) found that partitioning was probably most important in peanut.

Duration of transport into the cottonseed could be a serious developmental constraint if that period were relatively short. Despite the suggestions of the early breakage of the funiculus, which supplies the developing seed with nutrients (Ihle and Dure, 1972; Dure, 1975), it appears that developing cottonseed receive some assimilate essentially until maturity. If the assimilate supply to the seed stopped at 32 DPA, the remaining 16 to 20 days of seed development would involve only the metabolic alteration of previously obtained assimilate. This would have some very interesting biological implications. Pinkhasov (1981) reported movement of ^{14}C -assimilate into bolls at least until 45 DPA. Benedict *et al.* (1976) and Benedict *et al.* (1980) also reported incorporation of ^{14}C -assimilate into cotton lint until at least 45 DPA. The influx into bolls and incorporation into lint and other fruit structures plotted vs. boll age are basically bell-shaped curves with low levels near maturity, but there is no indication that influx ceases.

SUMMARY

Developing cotton bolls receive most of their assimilate from their subtending leaves or other leaves on the same sympodium. Other tissue, such as bracts, contribute a small portion of the boll's assimilate.

Photosynthesis has been found to limit cotton yields. Therefore, increased assimilate production is a desirable breeding goal, if gains are not negated by unfavorable changes in harvest index. It is interesting to note that at least in young leaves, low sink demand may reduce photosynthesis. Other sources of increased productivity may include reducing "wasteful" flower and fruit production and partitioning more photosynthate to reproductive growth. Both areas have limitation, however: (1) continued fruit production into the late season provides a hedge against total crop failure and may be accompanied by the development of needed leaf tissue; and (2) there is probably some minimum vegetative framework which is necessary for optimum plant function which can be exceeded if harvest index is increased too far. Transport of assimilate to bolls become more efficient when source-to-sink distances are shortened, but again this miniaturization must become counter-productive at some point. There is probably, at best, a 2-day reserve of assimilate under conditions of no photosynthesis. Although

starch may be detected in leaves, there is good evidence that remobilization declines as the plant and leaves age.

Correlation of sink size to sink strength is probably coincidental to metabolic activity of the large sink. While size may be useful for crop modeling, the related metabolic activity should be characterized to prevent over-simplification of the model. Influx of assimilate into the developing cotton fruit parallels synthetic activity through the development period. This is a bell-shaped relationship which is low in very young and nearly mature bolls and high at and following the mid-point in development.