Chapter 16

CARBOHYDRATE PRODUCTION AND DISTRIBUTION IN COTTON CANOPIES

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INTRODUCTION

The photosynthetic fixation of CO_2 by leaves of the canopy and the distribution of that carbohydrate among growing organs is, of course, the basis for crop productivity. The description of the carbohydrate distribution has been a very active area of research since Eaton and Rigler (1945) made a very comprehensive study of the interaction between light intensity and nitrogen nutrition with the growth, fruiting, and carbohydrate status of cotton plants. The most comprehensive versions of the modern computer simulations of the cotton crop are COT-CROP (Jones *et al.*, 1980) and GOSSYM (Baker *et al.*, 1984). These materials-balance models simulate carbohydrate production and use by the developing canopy. Reduction of the carbohydrate supply by stresses of various kinds (see Chapter 19) and the distribution of that carbohydrate in respiration and organ development are calculated by these dynamic models in attempts to simulate the performance of the crop. The fact that GOSSYM requires a computer with large (128 K) memory indicates the complexity of the dynamics of known chemical and physical interactions which produce a cotton crop. Perhaps it is remarkable that production is as reliable as it is. This chapter will outline the parameters which have been observed for carbohydrate production and utilization within field stands of the crop.

CROP GROWTH RATE

CARBOHYDRATE FORMATION

The single leaf rate of CO_2 uptake (CER) for cotton is in the upper range of the C_3 group. Values as high as 50 mg CO_2/dm²/hr have been reported (Muramoto *et al.*, 1965), but most reports have been in the range of 35 to 45 mg CO_2/dm²/hr (Patterson *et al.*, 1977; Elmore *et al.*, 1967; Mauney *et al.*, 1978). The conditions of growth for the leaves to be analyzed have pronounced influence on the values obtained in this measurement. Hesketh (1968) and Patterson *et al.* (1977) noted

that leaves grown under intense sunlight had a higher photosynthetic capability than those grown at lower light intensity. This effect was primarily the result of the intensity at which light saturation was observed. Leaves grown in maximum sunlight saturate at light intensity above sunlight, whereas leaves grown in shade saturate at a lower intensity.

The range of light experience for each leaf in the canopy is so varied that, even though there are adequate data to describe the light response curve of CO_2 uptake for individual leaves (Patterson *et al.*, 1977), the calculation of the canopy activity from single leaf data is inappropriate. Baker *et al.* (1978) pointed out that not only is the canopy made up of leaves with varied light intensity responsiveness, but also of widely varying leaf angles, sunflecks and photosynthetic organs other than leaves which contribute to the total CO_2 fixation.

Constable and Rawson (1980a,b) studied the translocation pattern in the cotton plant by determining the carbohydrate supply from each branch and comparing that supply with the demands of bolls present on the branch. They concluded that a major portion of the sink demand of maturing bolls must be met by import of carbohydrate from leaves elsewhere on the plant. The major contributors to this carbohydrate pool is apparently the mainstem leaves because of their large size and direct attachment to the vascular system of the mainstem (Constable and Rawson, 1980b).

MAXIMUM GROWTH RATE

Loomis and Williams (1963) calculated the maximum carbohydrate production by a canopy utilizing all the incident radiation to be 77 g dry matter/m^2/day. This value included a correction of 33 percent for respiratory loss. They felt that plant canopies with "several layers of leaves" should be able to achieve this potential growth rate even with the observed rates for CO_2 assimilation of 20 to 25 mg CO_2/dm^2/hr. They observed growth rates for dense stands of maize to be 51 g/m^2/day. Maximum crop growth rates for C_3 plants seldom exceed 40 g/m^2/day (Jones *et al.*, 1980). Baker and Hesketh (1969) made calculations of the maximum crop growth rate (CGR) of a cotton stand using weather information for July to October, 1966, in Mississippi. They used a value of 10 percent for maintenance respiration and a value of 56 percent for growth respiration. They calculated a CGR at 42 g/m^2/day on July 15 decreasing to 10 g/m^2/day on September 3 and increasing again as vegetative regrowth occurred. With all of this growth rate assigned to boll loading, they placed the maximum yield capability of that stand at 2850 kg/ha (5.9 bales/acre). If they assumed cloudless weather, their model predicted a maximum yield of 3650 kg/ha (7.6 bales/acre).

Maximum growth rates approaching these calculated values have been observed. Data taken in 1981 in Phoenix by Mauney (unpublished) are shown in Figure 1. These plots yielded 2380 kg/ha and had a maximum growth rate of the above-ground crop of about 25-30 g/m^2/day from July 25 to August 15. The 1981 growing season in Phoenix was characterized by rapid seedling growth due to
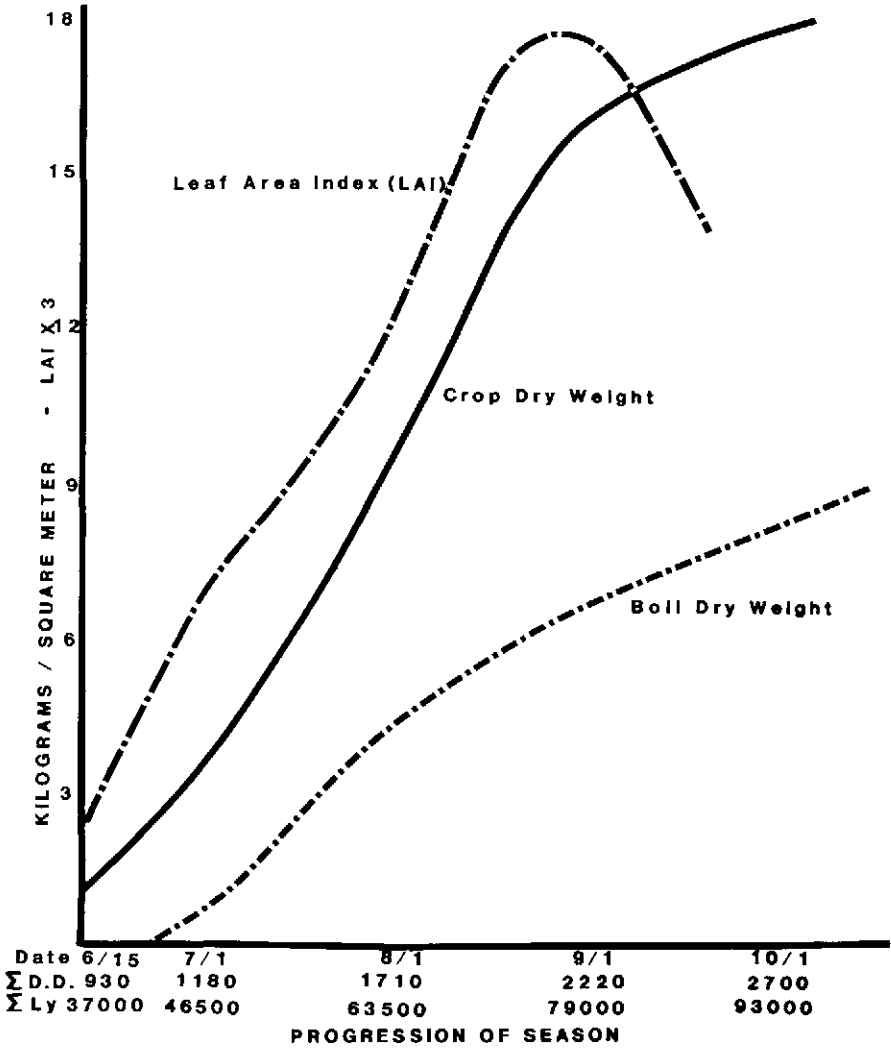
Figure 1. Relationships of crop dry weight accumulation above ground to leaf area index (LAI) and boll dry weight accumulation in Phoenix, Arizona, in 1981. This field produced a harvested yield of 5780 kg/ha seed cotton. Curves are smoothed average of six replications made at 7- to 10-day intervals and include abscised leaves, flowers and bolls. Heat units are in degree days (DD) with a 12.8C minimum and a 30C maximum using the triangulation method of averaging (Fry, 1983). Sunlight accumulation is in Langley's (ly) as measured by the U.S. Weather Bureau located 5 miles away. Sunlight and heat-unit accumulations are calculated from date of emergence, 4/10/81. Crop was *G. hirustum* cv. DPL 70 at a density of 80,000 plants/ha.

unusually high temperatures in April and May. The summation of heat units shown in Figure 1 are about 200 degree days (DD) higher at each date during July and August than the average year in Phoenix.

Canopy CO_2 fixation rates can be calculated from these growth data. Growth and maintenance respiration have been estimated by Baker and Hesketh (1969) and by Hesketh *et al.* (1971). The carbohydrate conversion efficiency is in the range .55 to .66 for both leaves and bolls. Therefore, 30 $g/m^2/day$ CGR requires 30 x 1.65 x 1.47 = 73 g $CO_2/m^2/day$ = 730 mg $CO_2/dm^2/day$ where 1.65 is the reciprocal of carbohydrate conversion efficiency and 1.47 is the CO_2/CH_2O conversion factor. This rate is similar to the maximum CO_2 uptake measured by Baker and Myhre (1968) who reported values greater than 700 mg $CO_2/dm/day$ on cloudless days in Mississippi.

SUNLIGHT INTERCEPTION

A principal determinant of the canopy carbohydrate production is sunlight interception. Walhood (1976) correlated the yield of variably-spaced plantings in California with the degree of sunlight interception during early season. When plant population was held constant at 84,000/ha and row spacing was 25, 50 or 100 cm, light interception changed dramatically in early season. On July 5, the 25 cm rows intercepted about 70 percent of sunlight while the 100 cm rows intercept-
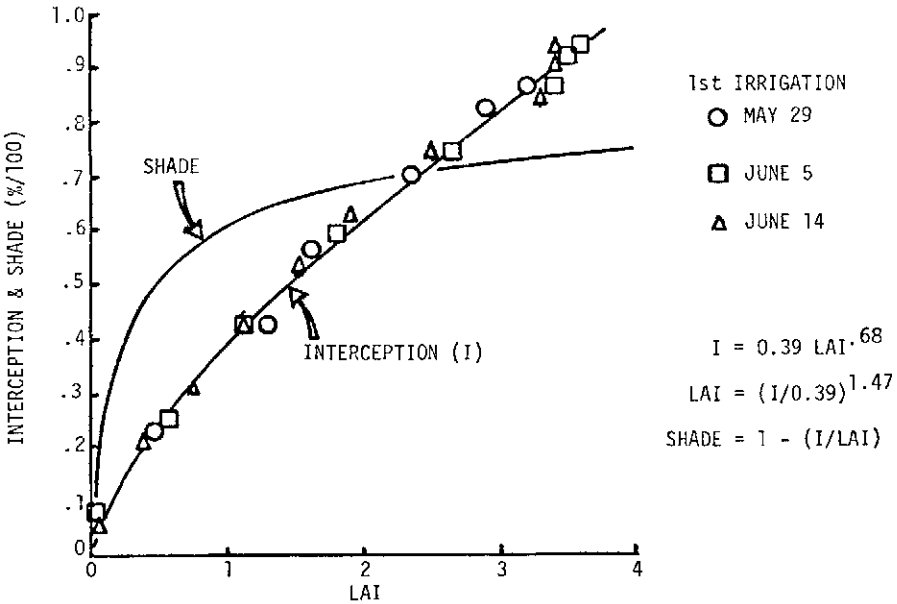

Figure 2. Percentage of light interception and shade for increasing leaf area index (LAI). From Fry (1980), used with permission.

ed 32 percent. As expected, the early-season and final yield in his short-season cultural practice correlated with the sunlight interception. The 25 cm rows had 42 percent more yield.

Fry (1980) correlated the midday sunlight interception with LAI (Figure 2) as the crop developed under several irrigation regimes. The regression line shown in Figure 2 is similar to that of Baker and Meyer (1966) who used row spacing and row orientation as the variables.

Until the canopy completely covers the furrow between rows, the row spacing causes a pronounced minimum in the daily interception curve at solar noon (Baker and Meyer, 1966). Because sunlight intensity is increasing while interception is decreasing, they observed a plateau in CER from 3 hours prior to 3 hours after noon. The regression between short-wave energy interception by the canopy and the uptake of CO_2 was linear (Hesketh and Baker, 1967). The heliotropic movement of cotton leaves (Lang, 1972) allows more of the leaf area to be normal to the sun than the calculations of deWit (1978) assumed. For this reason, when estimating the effects of row orientation on yield, Baker and Meyer (1966) measured interception directly rather than make a conversion from LAI. They concluded that the increase in interception due to North-South orientation of rows (compared to East-West) was not a significant factor in improving canopy efficiency.

BOLL LOADING AND BIOMASS ACCUMULATION

In view of the observation (Mauney et al., 1978) that starch accumulation can be a feedback mechanism for limiting CER when there is insufficient growth capacity to utilize all the carbohydrates leaves produce, one can speculate that the presence of bolls as sinks might enable greater carbohydrate translocation. This might result in higher canopy CER than if bolls were absent. This logic would hold however, only if stem, leaf and root growth were limited in sink capacity. And, as I remind myself and colleagues frequently, "Logic will get you nowhere" unless supported by data. The question of whether vegetative growth can absorb all available canopy carbohydrate has not been conclusively answered. In Table 1 are listed four experiments in which the flower buds were removed from plants and the change in total dry weight measured. All possibilities, i.e. increase (Dale, 1959), no change (Malik *et al.,* 1981; Nagarajah, 1975) and decrease (Eaton and Rigler, 1945) have been observed. Apart from the difference in outcome caused by the length of the experiments (Table 1), the different plant types, cultural conditions, and climate under which the observations were made could explain the lack of agreement. Dale (1959) explained the significant increase in weight of the disbudded plants by noting that the fruited plants ceased to grow when flowering began and gained only 8 grams of dry weight in the 84 days prior to final harvest, while the disbudded plants continued to grow vegetatively and add dry weight for 245 days. He, thus, called attention to the lack of simultaneous

Table 1. Response of cotton to the removal of all flower buds.

Growth period (days)	Plant weight (g/plant)		Reference
	Control	Disbudded	
92	835[1]	566[1]	Eaton and Rigler (1945)
105	50[2]	51[2]	Nagarajah (1975)
125	190[2]	226[2]	Malik et al. (1981)
245	150[2]	318[2]	Dale (1959)

[1]Fresh weight basis.
[2]Dry weight basis.

vegetative and reproductive growth in the cultivars he was studying. From his plant density (1 plant/ft in 36" rows), the dry weight accumulations can be converted to 1230 g/m², about .6 the weight of the stand shown in Figure 1.

Further analysis of the data in Figure 1 may add some understanding to the question of photosynthetic potential of the crop during boll-loading. In Figure 3 are graphed the crop growth rates of several portions of the stand as well as the total crop weight above ground. These data indicate that the maximum crop growth rate (30 g/m²/day) was attained only when leaves and stems were adding weight at near maximal rate and bolls were being filled. A possible explanation for this may be that the canopy was not fully intercepting all sunlight until early August (Figure 3). The rate of dry weight accumulation in the crop is roughly proportional to the fraction of light intercepted at solar noon. The coincidence of slightly higher crop growth rate per unit of sunlight intercepted during the rapid boll-filling period of July 1 to 15 may indicate an enhancement of crop CER by developing bolls. Those data are far from conclusive, however. During the prime period of dry weight accumulation (Aug. 1-15, Figure 3), the vegetative and reproductive organs each appear to be sinks adequate for deposit of the full carbohydrate output of the canopy. Since it is easy to imagine that a different climate might produce a different partitioning pattern (for instance, greater rate of leaf area expansion in a location with higher atmospheric humidity than Phoenix), the conclusive statement about the effect of boll loading on canopy carbohydrate fixation awaits data sets of the type shown in Figures 1 and 3 from widely dispersed locations.

CARBOHYDRATE DISTRIBUTION

The crop dry weight distribution shown in Figure 1 represents a crop which was similar in yield to the highest reported for furrow-irrigated cotton. Though yields of 2700 kg/ha have been reported from drip-irrigated fields (Briggs et al., 1983), lint yields greater than 2200 kg/ha are observed only rarely under furrow irrigation.
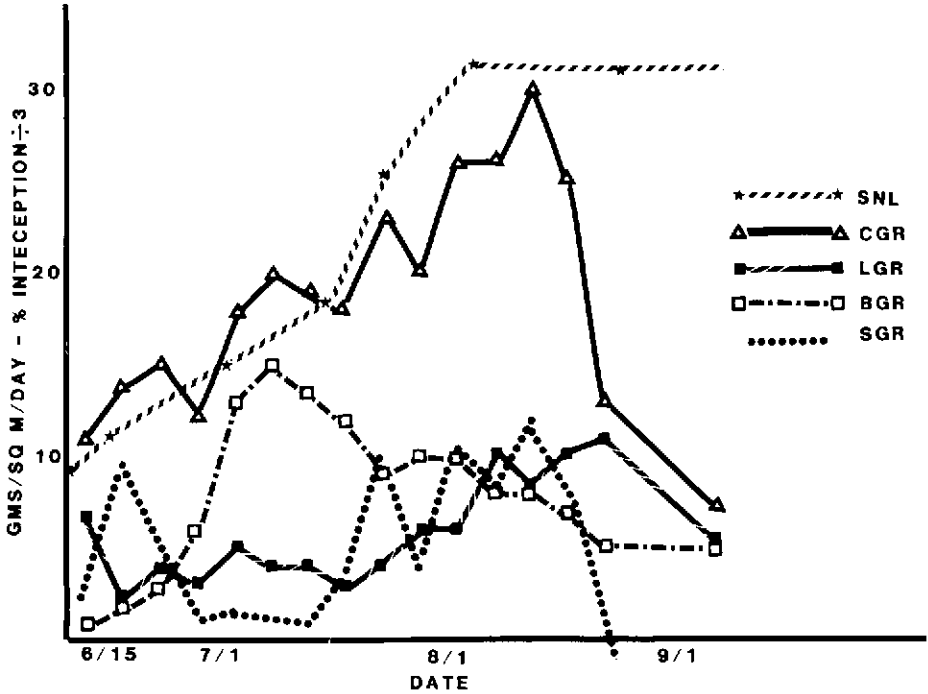
Figure 3. Rate of dry weight accumulation in portions of the standing crop described in Figure 1 and the percentage sunlight (SNL) intercepted at noon as estimated from Figure 2. Increases in crop weight (CGR), boll weight (BGR), and leaf weight (LGR) are from direct measurement. Changes in stem weight (SGR) were calculated by subtracting BGR and LGR from CGR.

Examination of Figure 4 shows that partitioning of the dry weight into fruits occurred in two cycles. From the onset of flowering until July 10, almost all the dry weight accumulation could be accounted for by increase in boll weight. From mid-July to mid-August, the dry weight increase was primarily in stems and leaves. After September 1, all dry weight increase was in bolls. This two-phase cycle of growth and reproductive partitioning is typical of irrigated southwestern areas with long, warm growing seasons. These areas have the highest productivity per hectare in the United States.

Baker and Hesketh (1969) assumed that for maximum productivity a vegetative canopy would be established by July 15, and that subsequently all dry weight accumulation would be in fruits.

This is not the strategy employed by highly productive real crops. Vegetative and reproductive growth occur simultaneously. It is significant that in the data of Figure 1 about 700 g/m² dry weight accumulated in the vegetative structure

subsequent to July 18 (when LAI of 3.0 was achieved). If this dry weight had been allocated to fruit, then the boll dry weight would have been 1500 g/m² for a lint yield of about 3600 kg/ha (7.5 bales/ac.). This is very close to the 3650 kg/ha estimated by Baker and Hesketh (1969) as the maximum potential for a cloudless season.
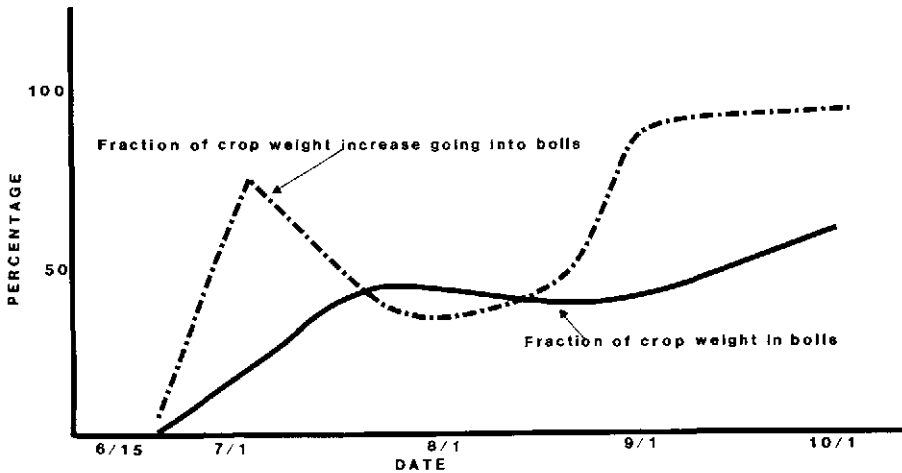

Figure 4. Distribution of dry weight accumulation into bolls during 1981 in Phoenix, Arizona (see Figure 1).

From this analysis it is apparent that the "inefficiencies" of the cotton plant are associated with the simultaneous vegetative and reproductive growth. The most productive canopies are those which allocate sufficient carbohydrate to vegetative growth to provide precisely the number of fruiting sites to absorb the remaining carbohydrate (see Chapter 2). In no instance would there be sufficient flowering sites on July 15 to enable all additional carbohydrate to be invested in fruits. A boll which matures on October 1 is the result of a blossom which opened on August 15 and was not visible as a square until July 25. Though the dry weight of the flower and fruit prior to anthesis is small (.2 g; Baker and Hesketh, 1969), leaf and stem development associated with each flower is the basis for the large non-boll dry weight investment.

The partitioning mechanisms which determine the fraction of dry weight assigned to vegetative and fruit growth are complex. The genetic tendencies of the crop for internode length, leaf size and shape, number of flowers per fruiting branch, etc., form a basis for partitioning. The water and nutrient status of the crop (Chapter 10) and environmental parameters such as temperature, sunlight and relative humidity change the capability of the crop to utilize carbohydrate for stem elongation and leaf expansion. The proximity of active source leaves to actively growing organ sinks appears to play a major role in determining the fate

of the carbohydrate from that source (Chapter 22). The growth habit of the plants in a cotton canopy is opportunistic. Those organs genetically and environmentally capable of growth which have favorable proximity to active leaves will be the organs to receive the majority of the available carbohydrate. The resultant of all the individual partitioning equations is the dry weight balance of the crop. Genetic and cultural strategies to improve the partitioning efficiency of the crop must take into account the dynamic nature of the interaction.