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MOLECULAR BIOLOGY AND PLANT PHYSIOLOGY

Carbon Allocation in Cotton Grown in CO_2 Enriched Environments

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ABSTRACT

Many studies have used CO_2-enriched environments to identify the factors limiting growth and productivity of the cotton crop. This review focuses on the allocation of carbohydrates within the plant in these environments. Three pools of carbohydrates have been shown to be altered significantly by CO_2 enrichment. 1) Leaf starch is increased during the day and mobilized for night utilization; 2) starch deposition in the stems increases during the juvenile period of growth and is utilized during the boll filling period, and 3) starch deposition is increased in roots during the juvenile and early fruiting period. This enables the roots to remain more active during the heavy demand of fruit maturation. The expansion of these three pools of deposition enables the cotton crop to utilize the higher photosynthetic rate to a greater degree than other crops. The activity in these pools determines the growth and productivity of the crop at ambient CO_2.

John Hesketh (Hesketh et al., 1972) was one of the first to suggest that measuring the growth and partitioning of the cotton plant at elevated CO_2 would provide clues about the factors which control and limit productivity of the crop. That began a series of developmental studies which resulted in writing the process-based simulation model GOSSYM (Baker et al., 1973) which was extensively reviewed by Baker and Baker (2010).

The exhaustive review by Krizek (1986) identified cotton as one of the most responsive crops to CO_2 enrichment. He reported that several studies had shown that in short-term exposures there was a linear increase in photosynthetic rates (P_n) with increasing CO_2 up to 660 ml l^{-1} (Wong, 1980). In experiments with long-term exposure, the rate of increase is much less (Harley et al., 1992; Sasek et al., 1985). Mauney et al. (1979) reported an increase of 10-14% in P_n with a 91% increase in CO_2 in greenhouse exposures. Idso et al. (1994) observed a 27% increase in P_n due to a 48% increase in CO_2 in field observations. In long term (80 day) exposures in plastic enclosures (SPAR units) Reddy et al., (2003) observed a 38% increase in leaf P_n when CO_2 concentration was doubled. Zhao et al. (2004) and Zhao et al. (2005) observed a 44% increase in P_n under similar conditions.

As a C3 woody perennial, cotton growth and development is limited by photosynthetically generated carbohydrate. Thus the effects of enhancing photosynthesis by CO_2 enrichment have attracted attention by numerous investigators. Mauney (2010) reviewed the variety of responses to CO_2 enrichment. By examining the partitioning of carbohydrates at elevated CO_2, the pathways of utilization can be defined, and processes which limit that production and utilization can be clarified. This review will concentrate on partitioning of dry weight in leaves, stems, roots, and bolls of the enriched crops.

Exposure to elevated CO_2 has been conducted in climate controlled greenhouses (Mauney et al., 1978), open-topped field enclosures (Kimball and Mauney, 1993), SPAR units (Reddy et al., 1999), and a free air CO_2 enrichment (FACE) facility (Mauney et al.,1994). Since the FACE environment was the least restrictive and most nearly represented the open field, those data will be emphasized in this review.

LEAVES

Diurnal cycling of starch is a typical feature of the carbohydrate budget of cotton leaves (Hendrix and Grange, 1991). Starch is deposited inside the chloroplasts, and as its concentration increases, its presence interferes with the photosynthetic process, and CO_2 fixation decreases as each day progresses (Mauney et al., 1979). That process is enhanced at elevated CO_2 concentrations resulting in starch content of CO_2 enriched leaves that is twice that of controls (Hendrix et al., 1994). Zhao et al. (2004) and Zhao et al. (2005) observed 3.6 and 4.2 fold increases,

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respectively, in the starch content of leaves in SPAR chambers exposed to doubling of CO_2 content for 80 days when compared with plants grown under ambient CO_2 concentrations for the same period of time.

The dynamics of starch cycling and loading of sucrose into the vascular transport system is very complex and varies with environmental factors, leaf age, and boll load (Hendrix, 2010). Baker and Baker (2010) concluded that phloem loading and translocation of carbohydrates was not a limitation to growth of cotton. That conclusion was based on daily production and use of the carbohydrate. On a shorter time scale, however, the data indicate that either the chloroplast membrane or the rate of travel of sucrose in the vascular system does limit the movement of the photosynthate away from the site of fixation. Concentration of sugars in leaves and stems (Mauney et al., 1979, Hendrix et al., 1994) and petioles (Chang, 1980) did not correlate with photosynthetic activity during the day or with CO_2 enrichment. Starch does build up in the chloroplast as the day progresses (Hendrix and Huber, 1986) and seems to inhibit the photosyntetic process (Arp, 1991; Mauney et al., 1979).

When cotton plants were transferred into a CO_2 enriched glasshouse environment, the P_n initially doubled compared to the ambient rate, but as starch increased over the following three days, P_n decreased to about 25% higher than plants under ambient conditions (Fig. 1). That rate increase was confirmed in the FACE treatment (Idso et al., 1994).

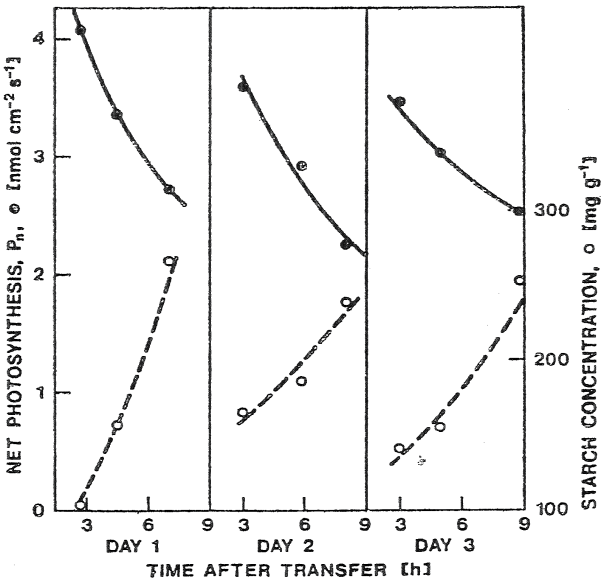

Figure 1. Change in leaf starch concentration and net photosynthetic rate, P_n, during three days following transfer from 330 to 630 ppm CO_2 (From Mauney et. al., 1979).

Vegetative growth and production of fruiting sites is similar in ambient, and CO_2 enriched plants during the juvenile and earlier flowering phase of development (Mauney et al., 1979; Kimball and Mauney, 1993; Mauney et al., 1994) (Fig. 2). During this time, excess carbohydrate is deposited as starch in the stems as well as the chloroplasts (Fig. 3). The CO_2 enrichment enabled about twice the concentration of starch to be stored under both well-watered and mild water-stress conditions.

Data from the 1991 FACE experiment shows that on day of year (DOY) 185 (Days after planting, DAP, 79), when flowering began, there was twice as much stored starch in the stems of enriched plots compared to ambient (40 vs. 20 mg/m, Fig. 3). Thereafter, as boll loading increased demand for carbohydrate, the starch level in both treated and control plots decreased until on DOY 240 (DAP 134) there was no starch found in stems of any plots. Thereafter, starch deposition returned to approximately twice the concentration in the enriched treatment as in controls.

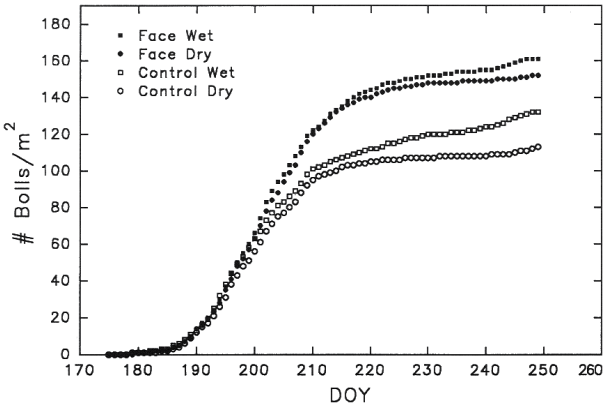

Figure 2. Cumulative load of harvestable fruit (bolls) on cotton plants in the control and FACE treatments in the well-irrigated (Wet) and water-stressed (Dry) plots. Data are from tagged flowers of the plots grown in1991. All points are the average of four replications. (From Mauney et. al., 1994).

ROOTS

Storage of starch in roots is less pronounced at any stage than in stems (Fig.3). However, root activity was enhanced by enrichment in a way which allowed for greater production of bolls. Prior et al. (1994) observed that taproot length, volume and weight increased by 18%, 36%, and 60%, respectively, on DOY 214 (DAP 108) in the 1991 FACE exposure to 550 ppm CO_2. Day 214 was well into the fruiting period of the crop in 1991 (Fig 2). The authors found that on that day fine root density was increased by 58% at a distance of 0.5 meters from

the plant row (i.e. mid row) for plants exposed to a CO_2 enriched environment.

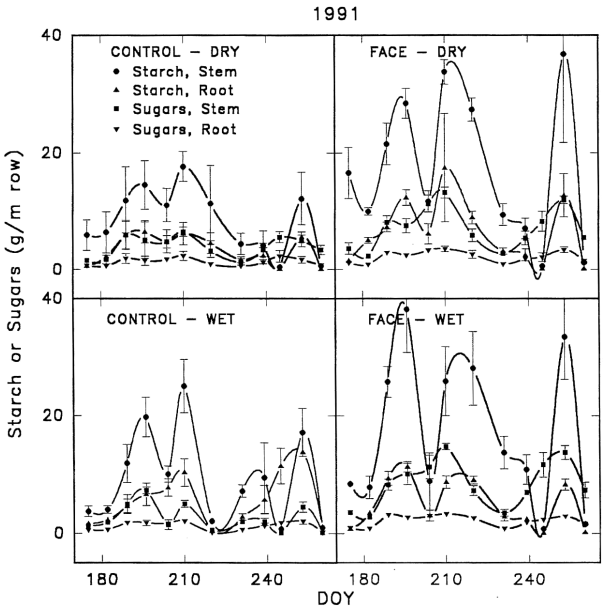

Figure 3. Soluble sugars and starch in dried taproot and stem tissue collected in destructive harvests at various times during the 1991 growing season. (From Hendrix et al., 1994).

Mauney et al. (1994) compared the effect of enrichment on the root/shoot ratios throughout the 1991 experiment (Fig 4). They found that beginning at DOY 180 (DAP 74), when flowering began, the root shoot ratio was consistently greater in the enriched plots. These measurements focused on the taproot weight, but Prior et al. (1994) noted that fine roots also had greater density.

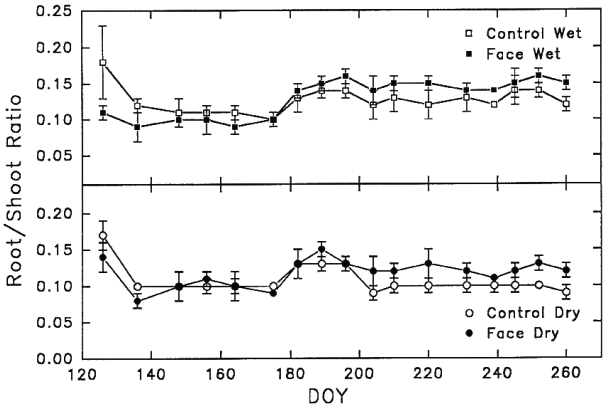

Figure 4. Root/shoot ratios throughout the growing season for the cotton crop grown in control or FACE conditions in the well-irrigated (Wet) or water-stressed (Dry) plots in 1991. Data are the ratio of the dry weights of roots which could be pulled from the soil divided by the dry weight of stem and leaves. Data are average of four replications. Vertical bars are the standard error for each point. (From Mauney et el., 1994).

One of the causes of cessation of flowering (cutout) is the competition for carbohydrates between vegetative growth, roots and fruiting (Mauney, 1986). This dynamic relationship is demonstrated clearly by examining the partitioning of dry weight during early fruiting in the CO_2 enriched treatment.

Table 1 shows that in the 1991 FACE experiment (Mauney et al., 1994) in the water stressed treatments (Control Dry, CD, and FACE Dry, FD) boll biomass gain was greater than total biomass gain. For example, bolls in the CD treatment gained 10.7 g/d dry weight while the crop gained 10.2 g/d. That is, more dry weight was added to bolls than was added to the crop! That means that starch was mobilized from stems and roots and moved to fruits. This strong demand for carbohydrate by the bolls coincides with the slowing of production of leaves and in the formation of additional flowering sites (Mauney et al., 1978).

Table 1. Dry weight partitioning within the cotton crop during selected time periods of the 1991 season. (From Mauney et al., 1991)

	Treatments			
	CD	**FD**	**CW**	**FW**
Time frame	**210-231**	**204-220**	**204-231**	**204-220**
Biomass gain ($g\ m^{-2}\ day^{-1}$)	**10.2**	**17.6**	**14.6**	**18.2**
Boll mass gain ($g\ m^{-2}\ day^{-1}$)	**10.7**	**17.9**	**12.7**	**16.6**
Partitioning (boll mass/total mass)	**1.04**	**1.01**	**0.87**	**0.91**

BOLLS

Individual bolls did not increase in rate of growth or final weight in the CO_2 enriched environment (data not shown). The increase in partitioning to fruit was through increase in the number of bolls in the final harvest (Fig 2). Delay of cutout resulted in the prolonged rate of active fruit set. This phenomenon has been observed in all the experimental means of CO_2 enrichment (Mauney et al. 1978, Kimball and Mauney, 1993, Reddy et al.,1999, Mauney et al., 1994, Reddy and Zhao, 2005). Because cutout is cyclic, that is the hesitation of flowering is followed by resumption of vegetative growth and renewed flowering and boll-set, the fractional increase in boll weight is determined by the length of the experimental treatment. In several of the open-topped chamber experiments the treatment was continued sufficiently long such that the ambient treatment set enough fruit

in the second cycle that yield differences between the CO_2 treatments were erased. In the two years of this FACE study the enrichment of the atmosphere from 330 to 550 ppm CO_2 caused an increase in yield of 42 to 51 % (Table 2). Since biomass production only increased 18 to 37%, it is clear that partitioning of the excess carbohydrate went to fruiting structures (Mauney et al., 1994).

SUMMARY

The vision of Hesketh that we could identify the limiting factors controlling cotton crop production by studying the effects of increasing P_n through CO_2 enrichment has been realized. Enrichment has identified three pools of carbohydrate deposition between photosynthetic production and boll-growth utilization.

1. Starch deposition in chloroplasts stores excess carbohydrate during day for mobilization at night.
2. Storage of starch in stems during juvenile growth is utilized during boll development to extend the prime period of boll set.
3. The deposition of starch in roots supports fine root activity, which enables water and nutrient uptake during the prime period of boll weight demand. This greater root activity delays cut-out, the negative feedback cycle which results in cessation of fruiting.

By expanding each of these pools, the enriched environment enables the cotton crop to utilize the higher photosynthetic rate to a greater degree than other crops. Activity of these pools determines the growth habit and final productivity of the crop at ambient CO_2.

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Table 2. Final yield of cotton crops in 1990 and 1991 from control (C) and FACE (F) treatments, which received wet (W) or dry (D) treatments. (From Mauney et al., 1994)

	Treatments				Ratio	
	CD	**CW**	**FD**	**FW**	**FD/CD**	**FW/CW**
1990						
Final harvest (bolls m^{-2})	**116**	**112**	**166**	**169**	**1.43**	**1.51**
Tagged rows (bolls m^{-2})	**122**	**118**	**152**	**179**	**1.25**	**1.49**
Destructive harvest (bolls m^{-2})	**124**	**121**	**157**	**177**	**1.27**	**1.46**
Total biomass (g m^{-2})	**1369**	**1412**	**1612***	**1895***	**1.18**	**1.34**
1991						
Final harvest (bolls m^{-2})	**112**	**122**	**159**	**174**	**1.42**	**1.43**
Tagged rows (bolls m^{-2})	**113**	**133**	**152**	**162**	**1.35**	**1.22**
Destructive harvest (bolls m^{-2})	**115**	**135**	**165**	**195**	**1.43**	**1.44**
Total Biomass (g m^{-2})	**1089**	**1386**	**1475****	**1896****	**1.35**	**1.37**

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