Chapter 3

PHOTOSYNTHESIS AND CARBON PARTITIONING / SOURCE-SINK RELATIONSHIPS

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INTRODUCTION

Photosynthesis is one of the principle biochemical processes underpinning plant growth and development. Because of its basic nature, it is intimately involved with reproductive growth and determining crop yields. Photosynthesis of a crop canopy can be broken down into three components: 1) leaf area development, 2) photosynthetic rate per leaf area, and 3) partitioning assimilates between vegetative and reproductive growth, or source-to-sink relationships (Krieg, 1983). The leaf surface area intercepts the solar radiation and allows for the photosynthetic conversion of that radiant energy into chemical energy. This production of chemical energy and the subsequent use of that chemical energy use to fix CO_2 into photosynthetic carbon assimilates constitutes the source side of yield development. The fruiting buds, flowers, and fruit development constitute the reproductive sink side of the yield equation, although other vegetative growing points can operate as secondary sinks. This interplay between the vegetative source and the reproductive sink can influence crop photosynthesis because the capacity for carbon assimilation can be somewhat regulated by the utilization of those photoassimilates in many crops (Krieg, 1983). The scope of this review chapter is to examine the intimate but complex relationship cotton photosynthesis (source) has with flowering and yield development (sink). The complexity occurs because major interactions change as the boll load increases with day length, temperature, and water availability decreasing as the season progress.

LEAF PHYSIOLOGY

The physiological changes a cotton leaf undergoes as it unfurls and expands have been well documented. Similar patterns of peak CO_2-exchange rates (CER) during leaf development were reported by Constable and Rawson (1980a) with the peak CER occurring between 13 to 15 days after leaf unfurling, and Wullschleger and Oosterhuis (1990a) who reported peak CER between 16 to 20 days after unfurling. This peak leaf CER occurred just before the leaf had become fully expanded (Constable and Rawson, 1980a). Both studies demonstrated that once this peak CER was achieved, it was then sustained for a few days before gradually declining as the leaf aged. Pettigrew and Vaughn (1998) also demonstrated that peak chlorophyll fluorescence variable to maximum ratios (Fv/Fm), an estimate of the photosystem two (PS II) activity, and leaf chlorophyll concentrations occurred during a similar time frame to that seen for the occurrence of peak CER. The slight differences in the timing of the events may have to do with the fact that field plants were utilized by Wullschleger and Oosterhuis (1990a) and Pettigrew and Vaughn (1998), while Constable and Rawson (1980a) utilized plants grown in the controlled environment of a greenhouse. The use of different cotton genotypes in these various studies could also somewhat contribute to these subtle timing differences reported. These observations have led to photosynthetic measurements in most subsequent studies generally being collected on the youngest fully expanded leaf of cotton plant to hit the period when the peak CER was occurring. Many researchers have generally wanted to hit the period of peak leaf CER with their photosynthetic measurement because they are often working under the assumption that any differences they were wanting to detect with their leaf CER measurements would be maximized during the period of peak CER. Measuring the youngest fully expanded leaf would also minimize the confounding factor of leaf age when assessing treatment effects on CER.

CER, LEAF AGE, AND GENETICS

The peak CER is not only determined by leaf age but also by genetics of the cotton. El-Sharkawy *et al.* (1965) reported leaf photosynthetic differences among numerous species of *Gossypium*. Beyond these species differences, a next logical place to look for photosynthetic variation is within a species, and particularly, among genotypes that possess different types of leaves. Across multiple studies leaf-type isolines of okra and super okra have exhibited increased lobing and reduced area of the leaves compared to the normal leaf-type (Wells *et al.*, 1986), but they have not shown consistent photosynthetic differences. Leaf-type isolines did not differ in $^{14}CO_2$ fixation (Kerby *et al.*, 1980; Karami *et al.*, 1980) or canopy CER when that photosynthetic rate was expressed on a leaf area basis (Pegelow *et al.*, 1977). However, there was an overall trend in these studies for the okra- and super okra- lines to have numerically higher photosynthetic rates. Wells *et al.*, (1986) reported that super okra and okra leaf-type isolines had reduced integrated canopy photosynthesis when expressed on a ground area basis due to their reduced overall leaf area production and canopy light interception when compared to the normal leaf-type isoline. Peng and Krieg (1991) also reported reduced late season canopy photosynthesis on a ground area basis for okra leaf cotton, but in contrast, they reported elevated canopy photosynthesis when expressed on a leaf area basis for okra leaf lines compared to normal leaf. Perry *et al.* (1983) also reported both okra and super okra leaf-types to have greater leaf CER than normal leaf-type. Similarly, Pettigrew *et al.* (1993b) found that the leaf CER of an okra leaf-type isoline was 22% greater than that of the normal leaf-type isoline counterpart. The leaf CER of super okra leaf-type isoline was also 24% greater than the normal leaf-type. Furthermore, Pettigrew *et al.* (1993b) reported the okra leaf-type line to have greater specific leaf weights (SLW), thicker leaves, and increased leaf chlorophyll concentrations than the normal leaf isoline. These aspects led them to conclude that the okra leaf-type isoline had a greater concentration of the photosynthetic apparatus per unit leaf area than the normal leaf-type isoline.

VARIATION IN PHOTOSYNTHESIS IN NORMAL LEAF-TYPE GERMPLASM

Genetic variation in photosynthesis can also exist within the normal leaf-type germplasm cotton lines. Rosenthal and Gerik (1991) reported that Upland (*Gossypium hirsutum* L.) cultivar Acala SJ-2 had a higher radiation use efficiency than either DPL 50 or Tamcot CD3H. Normal leaf-type genotypes that differed in their source-to-sink ratio were also found to differ in leaf CER by Quisenberry *et al.* (1994). They reported that leaf photosynthesis increased as the source-to-sink ratio was decreased. Furthermore, using a collection of 18 diverse normal leaf-type genotypes, Pettigrew and Meredith (1994) documented significant genotypic variation in leaf CER. Pettigrew and Meredith (1994) also observed a significant positive correlation between leaf CER and leaf chlorophyll concentration (0.768) and SLW (0.568). Beyond the *hirsutum* material, genetic variation in leaf CER also exists in the Pima (*Gossypium barbadense*) germplasm. Cornish *et al.* (1991) demonstrated that modern Pima lines had higher CER and increased stomatal conductance (g_s) than older, more primitive lines. They attributed the yield increases seen with the modern lines to the increased CER and g_s. In follow-up studies, Radin *et al.* (1994), Lu *et al.* (1994), and Lu and Zeiger (1994) indicated that yield improvements in modern Pima lines were associated with improved heat tolerance due to superior g_s and smaller leaf size.

VARIABILITY IN CER MEASUREMENTS

Another factor that can cause variability among leaf CER measurements is the decline in photosynthesis when measured on leaves during the afternoon compared to morning photosynthetic rates, even when measured under comparable sunlight conditions. A handful of studies have documented lower afternoon photosynthetic rates in both Upland (Pettigrew, 2004; Pettigrew and Turley, 1998; Pettigrew *et al.*, 1990) and Pima (Cornish *et al.*, 1991) cotton. Physiological reasons for this afternoon decline are still being debated. Processes that have been implicated in this afternoon decline for various plant species include: 1) high temperature stress (Baldocchi *et al.*, 1981; Perry *et al.*, 1983), 2) photoinhibition after exposure to the intense solar radiation encountered at solar noon resulting in damage to the photosynthetic apparatus (Powles, 1984), 3) a “down-regulation” of the photosynthesis in response to intense light conditions without damaging the photosynthetic structure by dissipating the excess absorbed photons as heat (Baker and Ort (1992), 4) end-product inhibition of the photosynthetic process due to the buildup of large carbohydrate levels during the afternoon hours (Nafziger and Koller, 1976; Peet and Kramer, 1980), 5) stomatal closure in response to an increasing H_2O vapor pressure deficit in afternoon hours (Bunce, 1982, 1983; Farquhar *et al.*, 1980; Pettigrew et at., 1990), and 6) nonstomatal photosynthetic inhibition caused by transient and localized water-deficit stress in response to high afternoon transpiration demand (Sharkey, 1984). The complexity of this phenomenon dictate that any or all of the aforementioned processes could be contributing to the afternoon photosynthetic decline observed at any particular time. Furthermore, when the photosynthetic decline actually begins during the day and the degree to which it inhibits photosynthesis is difficult to predict. For instance, this phenomenon has been observed to be more pronounced under moisture deficit conditions than under well-watered conditions (Pettigrew, 2004). Nonetheless, this afternoon photosynthetic decline must be taken into account whenever making photosynthetic measurements in any study. Researchers would be wise to complete their CER measurements prior to solar noon on most days to avoid this confounding effect.

LEAF CER AND YIELD

Even though theoretically there is an obvious connection between photosynthesis and reproductive growth, it has not always been easy to demonstrate the connection between leaf CER and yield production. Part of the problem lies in the fact that one would be using an individual leaf measurement to mimic a canopy phenomenon. Another problem is that you would be using an instantaneous measurement to mimic what happens during the entire growing season (Elmore, 1980). The perennial nature of cotton further complicates the issue because there has to be appropriate partitioning of the increased photosynthate into reproductive growth rather than vegetative growth to impact yield. Wells and Meredith (1984) were able to demonstrate that improved reproductive partitioning was responsible for much of the yield improvements in newer cotton varieties. Confirmation of this photosynthesis-yield relationship has also come from a series of source-to-sink manipulation studies (Pettigrew, 1994). Increasing the amount of sunlight intercepted by canopy leaves through either opening the canopy by pulling back adjacent rows or by placing reflective strips between the rows increased the lint yield by 17% and 6%, respectively. Furthermore, covering the plants with 30% shade cloth reduced the yield by 20%. Eaton and Ergle (1954) and Guinn (1974) also noted that lowering the light intensity resulted in increased boll and square shedding and also lower yields. Shading not only reduced yield but also reduced the fiber strength and micronaire of the fiber compared to the fiber produced under full sunlight conditions (Eaton and Ergle, 1954; Pettigrew, 1995). Increasing the photoassimilate supply by growing the cotton plants under elevated CO_2 conditions also has been shown to increase yields (Krizek, 1986). So yields can be increased whenever the total pool of photosynthetic assimilates is increased, either by increasing the amount of solar radiation that is intercepted by the canopy or by elevating the level of CO_2 the plants are exposed to during growth. By averaging the leaf CER over multiple measurements during the boll development period, Pettigrew and Meredith (1994) were able to demonstrate a direct connection between leaf CER and yield development for a diverse group of 18 genotypes. While increased photosynthesis can be a component of yield increases, it does not, in and of itself, guarantee a yield increase. The extra photo-assimilates produced with elevated photosynthesis must be directed to the reproductive structures rather than any of the potentially competing vegetative sinks, such as roots, stems, branches, or new leaf growth.

SINK STRENGTH AND PHOTOSYNTHETIC PERFORMANCE

Documenting the effect that sink strength can exert upon photosynthetic performance for cotton is a complex issue. This relationship is generally defined as a function of the source activity (photosynthesizing area × photosynthetic rate) and sink activity (number of actively growing sinks X the dry matter incorporation rate) (Krieg, 1983). It is simple to believe that as the strength of the total sink activity increases that there might also be a concurrent increase in the total source activity to feed the growing sink demand. Finding evidence to support this assumption has proven difficult. The results from multiple studies can be confusing to interpret and at times appear contradictory in nature. On the one hand, Quisenberry *et al.* (1994) reported that single-leaf photosynthesis increased as the source-to-sink ratio decreased, suggesting that the lower amount of source tissue was having to increase production to meet an increased sink demand. The altered source-to-sink ratios in the Quisenberry *et al.* (1994) study were accomplished with genotypes of maturity ranging from very early to very late and by also including a photoperiod sensitive line that would not flower during the growing season at that latitude. In contrast to Quisenberry *et al.* (1994), when fruit removal was utilized to increase the source-to-sink ratio, either leaf photosynthesis was unaffected (Pettigrew *et al.*, 1993a) or the radiation use efficiency was increased (Sadras, 1996). Using insect predation to implement their fruit loss, Holman and Oosterhuis (1999) reported the both leaf and canopy CER were increased when the plants suffered damage from tarnished plant bugs (*Lygus lineolaris* Palisot de Beauvois) and bollworms (*Helicoverpa zea* Boddic). They concluded that the improved canopy CER was due to greater light penetration into the canopy also produced by the insect infestation. Growth regulators can also be used to manipulate the source and sink relationships. Gwathmey and Clement (2010) reported that the growth regulator mepiquat chloride reduced leaf area per plant, while also increasing the number of bolls per leaf area. Reduced leaf area development from mepiquat chloride application was also reported by Hodges *et al.* (1991), but they also found higher gross photosynthesis for the mepiquat chloride-treated plants. Results from Hodges *et al.* (1991) tend to lend support to the Quisenberry *et al.* (1994) findings of increased photosynthesis with decreased source-to-sink ratios. It was primarily a reduction of the source material that decreased the source-to-sink ratios in the Quisenberry *et al.* (1994) work, because the sink size (boll weight plant^{-1}) was not consistently affected by the mepiquat treatments.

SYNCHRONIZATION OF PHOTOSYNTHESIS AND ASSIMILATE DEMAND

One of the reasons for the inconsistency in describing the relationship between photosynthesis and sink size or strength is that the temporal pattern of photosynthetic production for an individual leaf is not totally synchronized with the development and assimilate demand patterns of the nearby fruiting structure. Constable and Rawson (1980a) demonstrated the peak photosynthesis for a main-stem leaf occurred several days prior to anthesis of a 1st position bloom on the adjacent sympodial branch. During the filling and development of the boll, the photosynthesis of that leaf had already decreased substantially. The subtending leaf to that flower was in better synchronization as its peak photosynthesis occurred near anthesis, however, but it was not able to supply all the carbon needs of that developing boll by itself (Ashley, 1972; Constable and Rawson, 1980b). Utilizing a carbon budget model, (Constable and Rawson, 1980b) were able to calculate that considerable remobilization and movement of carbon between nodes and into and out of storage pools was needed to support the developing boll load. Wullschleger and Oosterhuis (1990b) confirmed this out of step timing between leaf photosynthesis and boll demand for assimilates with field grown plants. Constable and Rawson (1980b) further predicted that as the cotton canopy approaches cutout, a period of slowing vegetative growth occurs due to increased assimilate demand from the developing bolls, thus, the overall canopy photosynthesis would decline due to the aging and declining photosynthetic capacity of the individual leaves. This prediction was confirmed by the research of Wells *et al.* (1986) and Peng and Krieg (1991) who demonstrated that the canopy photosynthesis declined as the canopy aged. Unfortunately, this declining canopy photosynthesis is occurring during a period of greatest assimilate demand from the developing boll load. These results further confirm that the lack of synchronicity between assimilate demand of an individual developing fruit and the assimilate production from the nearby leaves ultimately causes the demand for photoassimilates by the developing boll load to be out of phase with the level of assimilate production by the cotton canopy.

REASONS FOR LACK OF SYNCHRONY

Part of the reason for the lack of synchrony between leaf photosynthetic potential and boll carbon assimilate demand is that the plant essentially cannibalizes its leaves by remobilizing its N-based components to feed the N needs of the growing bolls. Wells (1988) was able to clearly demonstrate this property by showing that, for all but the upper most leaves, the concentrations of chlorophyll, soluble protein, and ribulose bisphosphate carboxylase/oxygenase (Rubisco) decreased as the leaves advanced in age. Furthermore, he also demonstrated that leaves emerging during vegetative growth had higher levels of the N components when the leaves first reached full expansion than leaves that emerged during fruit development, when the reproductive sink for N assimilates is growing. By assessing the photosynthetic performance on leaves of plants from different planting dates on a mid-August measurement date, Pettigrew *et al.* (2000) were able to demonstrate that leaves from early planted plants had reduced leaf CER, soluble protein, and Rubisco activity compared to leaves from late planted cotton on that date. In contrast, they found that neither leaf chlorophyll concentration nor the chlorophyll fluorescence variable to maximum ratio (Fv/Fm) were altered by planting date. They concluded that N remobilization from the leaves to feed the developing boll load initially targets the proteins in the carbon fixation half of the photosynthetic equation and then later goes after the proteins and chlorophyll involved in light harvesting and the conversion of that sunlight into chemical energy.

IDIOSYNCRASIES OF PHOTOSYNTHESIS

Many of the idiosyncrasies intertwined with photosynthesis and crop yield in cotton are related to the fact that cotton is a perennial crop that is grown as an annual. While this perennial nature and indeterminate flowering pattern provides cotton with some flexibility in enduring short-term unfavorable environmental conditions, it also leads to the out of sync fruit development pattern with regards to photosynthetic production and further complicates the defoliation and harvesting process. Maintaining crop canopy photosynthesis for a longer duration might be a desirable pursuit because it could help to increase overall yield production since the level of photosynthetic production would be better timed to fulfill the current reproductive demand. Additional N fertilization has been suggested as a possible venue to maintain canopy photosynthesis because the remobilization of N out of the leaves to support the developing boll load was identified as a component involved in the photosynthetic decline observed late in the growing season. Bondada *et al.* (1996) were able to demonstrate higher rates of N fertilization increased canopy photosynthesis, delayed cutout, extended the duration of the cotton canopy and increased yields. Unfortunately, N fertilization in cotton can be a complex issue. In the Mississippi Delta, for instance, fertilization rates above 112 kg N ha^{-1} rarely elicit a yield response, but in California with its higher yield potential rates, higher than 112 kg N ha^{-1}, often produce yield increases. The nitrogen requirement for optimal yields is complicated because of the indeterminate growth habit of cotton and the complexity of N cycling in the soil. (Gerik *et al.*, 1998). While higher N fertilization may extend the duration of cotton canopy photosynthesis, it can also have negative consequences because it can create a lusher canopy that is more attractive to insects and cause complications for the defoliation process. Clearly any bolls lost to insect predation would create a disconnect between the higher canopy photosynthesis after additional N fertilization and yield production.

SUMMARY

Logically it would seem to be beneficial if cotton's photosynthetic production was better synchronized the with yield development. At the present time, however, there doesn't appear to be any obvious production technique to improve the timing of photosynthesis and yield production. The perennial aspect of cotton creates additional assimilate sinks and storage pools to ensure sufficient reserves will be available for new growth during subsequent seasons if the crop is not cultured as an annual and dies in the off season. This lack of synchrony between photosynthetic source production and reproductive sink demand creates the need for some assimilates from these secondary sinks and storage pools to be remobilized to support the growing fruit load. Because of this partial dependence on remobilized assimilate, a timing / distribution bottleneck could potentially occur in the assimilate supply / demand function during critical phases of reproductive growth and theoretically limit overall yield production. Conversion of cotton from a perennial plant to an annual plant could theoretically minimize the size or totally eliminate some of these secondary sinks and storage pools, and in the process free up some of those assimilates for further reproductive growth. There would still have to be adequate partitioning of these "freed-up" assimilates to reproductive growth to see any improvement on the yield front. Perhaps in the future, our friends in molecular biology and plant genomics could devote a portion of their efforts toward producing a truly annual cotton plant for the physiologists and agronomists to utilize.

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