The *Journal of Cotton Science 20:196–206 (2016)*
http://journal.cotton.org, © The Cotton Foundation 2016

MOLECULAR BIOLOGY AND PLANT PHYSIOLOGY

The Role of Temperature on the Diurnal Sucrose Source to Sink Balance

Toby R. FitzSimons and Derrick M. Oosterhuis

ABSTRACT

The diurnal fluctuations of carbon from its assimilation within the leaves, its export into the phloem, and its use in sink tissues has been studied in its individual parts for quite some time. In cotton (*Gossypium hirsutum* L.), the majority of the research concerning diurnal sucrose flux in response to temperature is for the most part greater than a quarter century in age, well before the introduction of modern cultivars. Additionally, diurnal research is lacking of any significant examination of any particular temperature profiles, making it difficult to compare responses from one treatment to another. This summary of research focuses on the diurnal flux occurring from both the source and the sink with special attention on four specific temperature profiles; low night temperatures, high night temperatures, low day temperatures, and high day temperatures. Due to the lack of suitable information inherent in some areas, information from other species was used as needed. It is the authors' intent that temperature dependent diurnal flux should be reexamined as modern cultivars continue to be developed.

There is a fundamental link between the assimilation, storage, and growth of a plant in relation to its source-sink relationship; ergo the connection of carbon usage and transport from the assimilatory (photosynthetic) source tissues to the sink (non-photosynthetic) tissues. During the day, triose phosphates of reduced carbon are manufactured during photosynthesis. These triose phosphates then follow several potential pathways depending upon the cellular needs at the time. If the cellular needs are high, then export of the reduced carbon into the cytosol is preferred. If assimilation exceeds demand, then starch production is preferred. At night, starch is broken down via hydrolytic and phosphorolytic pathways into sucrose and either exported to sinks or for immediate cellular use depending upon cellular needs (Weise et al., 2006). This relationship is especially important in cotton (*Gossypium hirsutum* L.), since cotton fibers are composed near exclusively of cellulose, a polysaccharide composed of thousands of interlocking β-(1→4)-D-Glucose units whose sole carbon building source extends from sucrose. Furthermore, the cotton fiber qualities of length, strength, and micronaire are directly influenced by the concentration of photoassimilates transported to the developing boll.

When conditions are favorable with adequate light, moisture, and nutrient availability, a developing boll will acquire more than 60% of the photoassimilates needed for fiber growth from its subtending leaf (Ashley, 1972; Constable and Rawson, 1980). To supplement the remaining 40%, translocation across the entire plant becomes necessary. However, early vegetative growth is the preferred sink and outcompetes reproductive sinks. It is not until the twelfth node that the vegetative growth rate plateaus, and carbohydrate is diverted towards reproductive units without major translocation between branches (Wullschleger and Oosterhuis, 1990). This translocation is important to maintain sucrose availability to developing sinks. Temperatures can have a significant impact on the plant's ability to transport sucrose, resulting in potential deficiencies that affect final crop productivity (Stewart, 1986).

Cotton has an optimal temperature range for carbohydrate production, and temperatures outside of the optimal result in increased square and boll shed (Guinn, 1982). This particular intolerance to extreme temperature has been a major area of research in regards to the diurnal flux of carbohydrate. For instance, cotton has an upper optimal growth temperature of about 32ºC (Burke et al.,

T.R. FitzSimons and D.M. Oosterhuis, University of Arkansas, Department of Crop, Soil, and Environmental Sciences, 1366 West Altheimer Drive, Fayetteville, AR 72704
*Corresponding author: Toby FitzSimons, tfitzsim@uark.edu

1988), achieves maximal photosynthetic rates at 33ºC (Bibi et al., 2008), and a maximal boll development rate at 30ºC (Reddy et al., 1991). On the other hand, as temperatures dip below 23.5ºC, the kinetics of enzymatic reaction rates decrease, hampering both vegetative and reproductive growth and development (Burke et al., 1988). These limitations are a hindrance to growers and breeders as temperatures on both sides of the optimum range are quite common in the Mississippi River Delta regions of the United States. Further complicating this sensitivity to temperature extremes is that supraoptimal temperatures in the summer coincide with cotton's most heat sensitive period of development, reproduction (Reddy et al., 1992; Snider et al., 2009; Zhao et al., 2005) .

In Figure 1, weather and planting data from the University of Arkansas Lon Mann Experiment Station in Marianna, Arkansas was overlaid with regional averages of squaring and flowering percentages of fields in the region. The station's central location in cotton growing areas of the Mississippi River Delta is evident in that squaring and flowering dates for the station coincide with state averages for squaring and flowering. On average, high temperatures above the 30ºC threshold for negative reproductive effects overlap with squaring and extend well into flowering. Consequently, locations further south would expect to reach high temperature thresholds earlier in the growing season than in the centralized location of Marianna, AR.

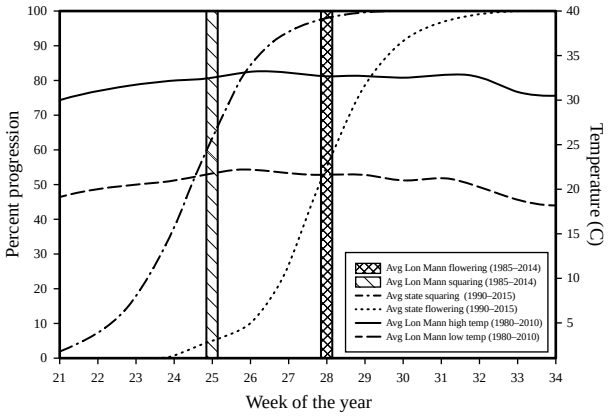

Figure 1. Temperature profile of the University of Arkansas Lon Mann Research Station in Marianna, AR overlain with the average flowering and squaring data from 1990 to 2010, and state flowering and squaring averages for the state from 1990-2015. Above 30ºC, negative impacts to cotton yield begin to occur and squaring and flowering all occur at or above this temperature threshold.

Normally, temperatures in the Mississippi River Delta deviate significantly from these climatological average temperature maximums and minimums. It is not uncommon for areas in the region to exceed 38ºC for several days regularly during the summer season (Boykin et al., 1995). When temperatures exceed the optimum temperature threshold of enzymes necessary for photosynthesis, overall photosynthetic efficiency declines. An example of this is rubisco activase, responsible for the activation of the enzyme rubisco (Ribulose-1,5-bisphosphate carboxylase/oxygenase), a key component of carbon fixation. When temperatures exceed 35ºC, rubisco activase activity is hindered, limiting photosynthetic efficiency (Carmo-Silva and Salvucci, 2011; Crafts-Brandner and Salvucci, 2000). However, more recently it has been emphasized that higher night temperatures should also be reexamined as they diminish cotton's overall rate of growth (Loka and Oosterhuis, 2010).

Similarly, suboptimal temperatures can also hinder proper growth and development. The lower thermal limit for positive growth rates is 20ºC (Reddy et al., 1991) and metabolic rates are not fully realized below 23ºC (Burke et al., 1988). These temperatures are common during the early growing season. Hesketh et al. (1972) noted that the interval between leaf progression was near three times as long at 18ºC compared to 30ºC. Further, photosynthesis was 40% lower for plants grown at 20ºC in full sun versus plants grown under optimal temperatures with full sun, due to increased photoinhibition (Königer and Winter, 1993), most likely due to disruption of enzymatic activities affiliated with the photosystem complexes (Allen and Ort, 2001).

It is with this thermal bounding in mind that we examine the effects of temperature on the diurnal carbon balance within the cotton plant. Photosynthetic carbon assimilation occurs only under light conditions but the growth, maintenance, and adaptation to the environment occurs throughout all hours (Mutsaers, 1976; Walter and Schurr, 2005). Researchers within the last quarter century have also begun to examine and understand the complex relationships that sucrose and starch may have as key players within certain areas of cell signaling during the diurnal cycle (Granot et al., 2014; Hummel et al., 2009; Lunn et al., 2006). What we seek to accomplish in this paper is to provide a brief examination of diurnal carbohydrate fluctuations focusing on the production of sucrose and starch and its use as affected by different profiles of temperature stress.

BASIC CIRCADIAN RHYTHM OF THE PLANT

During the day, light cast onto the leaves stimulates the photosynthetic apparatus that channels photonic energy into photosystems I and II where the solar energy is converted into chemical energy. This chemical energy coupled with CO_2 is assimilated into sugars that are either stored within the leaf or used for subsequent export. The primary storage compounds within the leaf are starch, which is stored within the chloroplast and is not available for immediate utilization, and as sucrose, present within the cytoplasm and either used immediately or exported via phloem. At night, carbon assimilation ceases and the accumulated starch within the chloroplast is hydrolytically broken down into maltose and exported into the cytoplasm where it is further transformed into sucrose and glucose. This sucrose is again either used immediately for cellular needs or exported via the phloem to awaiting sinks (Weise et al., 2004). The overnight conversion of starch into sucrose is dependent upon the starch concentration at nightfall, so that by dawn only 5% of the initial starch reserves remain within the chloroplast. The process is again repeated as light begins to strike the photosynthetic apparatus and carbon fixation occurs (Hendrix and Grange, 1991; Hendrix and Huber, 1986; Lu and Sharkey, 2006; Weise et al., 2006).

This brief summary of the diurnal process belies a wealth of biochemical and signaling processes that maintain a steady supply of energy for the plant. The production and storage of created carbon products have innate control mechanisms that allow for a precise amount of energy to be available for the plant under normal conditions. For example, starch synthesis and storage rates are directly related to the carbon needs of the tissue at night. In longer days, starch accumulation rates decrease, as there is more time to create starch. While under shorter day lengths the rates of starch accumulation and subsequent storage increase. This accumulation is further refined based upon the amount of starch remaining in the chloroplast by dawn, which correlates with tissue respirational needs the previous night (Graf and Smith, 2011). Examinations in *Arabidopsis* have shown that starch synthesis is inversely proportional to the requirements needed from the previous night. And subsequently, the rates of starch hydrolysis are also dependent upon the length of the previous dark period (Gibon et al., 2004).

Upon first light, the rubisco inhibitor CA1P (2-carboxy-d-arabinitol-1-phosphate phosphatase) which has been tightly bound during the course of the night is dephosphorylated by rubisco activase and carbon assimilation initiated (Servaites, 1990). Sucrose synthesis rates begin to rise slowly as more CA1P is dephosphorylated and sucrose is directed into amylopectin which begins to accumulate followed by increasing concentrations of amylose (Chang, 1979). In the early afternoon, sucrose production begins to diminish as the amount of inorganic phosphates within the stroma decreases and subsequent rates of sucrose-phosphate synthase (SPS) are lessened (Huber and Huber, 1996). Stitt et al. (1988) indicated that SPS activities are proportional to concentrations of sucrose in the cytosol, with greater concentrations hindering SPS activity and subsequently promoting increased starch synthesis rates within the stroma.

This work is consistent with previous work performed on cotton leaves by Hendrix and Huber (1986) which showed that SPS activities decreased in the early afternoon with sucrose export rates showing similar decreases throughout the night until the early morning. Figure 2 is adapted from the Hendrix and Huber (1986) paper showing diurnal variations of the carbon exchange rate within the leaf, the sucrose activase rates, and subsequent sucrose export. By early afternoon, carbon exchange rates have peaked and decrease into the evening, followed by decreases in the starch accumulation rate and sucrose export. At night, sucrose export rates initially are very low, but subsequently adjust to demand, decreasing linearly until dawn. Further, the starch accumulation rate shows a steep negative trend early in the night, as photosynthetic activity ceases until the following dawn when starch accumulation rates increase rapidly.

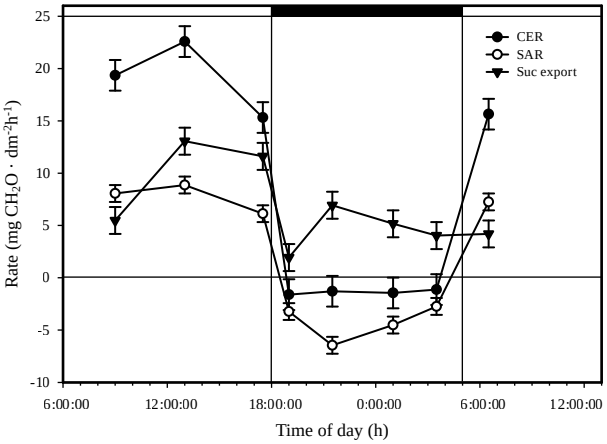

Figure 2. Adapted from Hendrix and Huber (1986) showing the diurnal variations in the carbon exchange rate (CER), the sucrose activase rate (SAR), and sucrose export of the leaf (Suc Export) of greenhouse grown cotton (cv. Coker 100). The dark bar at the top indicate the dark period of the diurnal cycle. Error bars indicate the least significant difference at the p = 0.05 level.

Hendrix and Grange (1991) reported that starch is not broken down during the illuminated hours, and that all carbon exported at night came from starch reserves. Additionally, if nightly reserves were depleted then sucrose production the following light cycle took precedence as the first resource pool filled rather than starch. At night, concentrations of soluble sugars within tissues remain constant as starch is slowly broken down. The rate of starch hydrolysis and sucrose export is adjustable, as it is dependent upon the amount of starch stored at dusk. Hendrix and Grange's (1991) results detailed that if dusk starch concentrations were below 75 µg per cm^2 then carbon export did not occur during the night. Moreover, as pre-dusk concentrations of starch increased, the nighttime rates of sucrose export also increased at a linear rate dependent upon initial starch reserves and sink demands. For instance, if daily starch accumulations were 100 µg per cm^2, then starch hydrolysis would ration 25 µg per cm^2 for the sucrose export over the course of night. By dawn, if starch reserves had not been completely exhausted, there is a short temporary inhibition of growth and carbohydrate utilization as chemical energy pools are replenished (Gibon et al., 2004). However, if dark conditions continued or starch reserves were depleted, then the plant transitioned into an energy starvation state. During this process, transcriptional changes occur that impede growth during the daylight cycle as more energy is transferred into starch reserves rather than the export of sucrose to awaiting tissues (Smith and Stitt, 2007; Usadel et al., 2008).

Weise et al. (2004) identified that the sugar maltose was the predominate carbon form exported from chloroplasts at night. Thus, they hypothesized that the genes that dictate maltose export and regulation could be directly influenced by both day length and temperature. This was later expanded upon in the summary by Lu and Sharkey (2006) which provided stronger evidence supporting the influence of day length and temperature on the genetic control of circadian maltose regulation that could adjust to changing environmental conditions.

EFFECTS OF COOL TEMPERATURE AT NIGHT

During the season, night temperatures can fall below the lower optimum of 20°C on a consistent basis, particularly in more temperate growing areas. Warner et al. (1995) demonstrated that cotton leaves exposed to cooler conditions exhibited significantly lower overall concentrations of starch when compared to unstressed leaves. At night, starch catabolization occurs at a greatly reduced rate and leads to higher starch concentrations at the beginning of the night cycle compared to those plants in slightly warmer conditions. Additionally, photosynthetic rates in cooler night plants were only 77% of those rates in warmer night conditions. The conclusion was that cooler night temperatures alter carbohydrate production during the daylight hours.

Work in soybean (*Glycine max* L.) from Van Heerden et al., (2003) indicated that cool night temperatures reduce overall photosynthetic CO_2 assimilation rates and CA1P activation. Further, rubisco activase during the following light cycle indicated no net decrease in activity. It was surmised that the reduction in CO_2 assimilation rates may be related to depression of certain enzymatic pathways, particularly those involving fructose-1,6-bisphosphatase for as much as 8 hours into the warmer light cycle. This was supported by Singh et al., (2005) who noted a 12% reduction in cotton leaf photosynthetic CO_2 assimilation activities the day following a cool night (9 - 12 °C). The activity reductions were temporary and resulted in no net decrease in CO_2 assimilation after two days. Subsequent new leaves did not display reduced assimilation rates, suggesting a possible acclimation effect to the cooler temperatures.

Of interest from the work by Singh et al., (2005) is that starch accumulation was also significantly inhibited across all cotton varieties under cool night temperatures. Rates of CO_2 assimilation did not differ from the control either. This was in contrast to previous work from Warner and Burke (1993) that indicated increases in starch content due to diminished metabolic rates and growth rates. However, the night temperatures in Warner and Burke's experiment (20°C) were not as low compared to Singh's experiment (decreasing from 16.7 to 9.8°C). Warner and Burke also found a net decrease in chlorophyll fluorescence the following day, which is a measure of the efficiency of photosystem II and can directly impact carbon assimilation (Krause and Weis, 1991).

Sucrose export from the leaves is controlled by a temperature-dependent conversion of starch to sucrose, which has direct influence upon phloem loading (Hendrix and Huber, 1986). Concentrations of adenosine triphosphate (ATP), and respiration rates in leaf tissue were significantly diminished as temperatures fell below 15°C, but sucrose levels

within the tissues remained similar to the control suggesting an overall slowing of growth as sucrose levels matched metabolic needs (Lawrence and Holaday, 2000). Many woody perennials, like cotton, at low temperatures can constrict plasmodesmata linking mesophyll cells to phloem cells reducing active loading potentials, further increasing the concentrations of sucrose within tissues (Gamalei et al., 1994). This can have the negative effect of reducing the photosynthetic rates significantly due to a reduced need for photoassimilates (Goldschmidt and Huber, 1992).

EFFECTS OF HIGH TEMPERATURES AT NIGHT

The effects of increased night temperatures can have a significant impact on the diurnal cycle. Electron flow during the day initiates increased plastoquinone pools and xanthophyll pathways that mitigate excess energies, protecting the photosystem. These activation pools are reduced overnight by respiratory oxidative damage under normal temperatures. However, increased nightly temperatures rapidly decrease these antioxidant pools at a significantly greater rate, increasing the possibility for reactive oxygen species to damage the photosystem (Feild et al., 1998; Marutani et al., 2012); Sharkey, 2005) .

High night temperatures also increase respiration rates of the plant, increasing by as much as 20-46% for each 10ºC increase (Frantz et al., 2004). Soluble carbohydrate concentrations were examined under controlled environmental conditions for both acute and chronic high night temperature stress by Loka and Oosterhuis (2010). Under acute conditions, sucrose and hexose levels remained similar to the control leaves, while under more chronic conditions the levels of sucrose were significantly less than the control. Respiration rates also increased with temperature and pools of ATP were significantly reduced, indicating a greater draw on energy pools. Warner and Burke (1993) noted that after the first night of acute increased temperatures, starch levels were exhausted prior to sunrise, due to increased respiration. Research from Hewitt et al. (1985) found that soybean leaves exposed to chronic high night temperatures had significantly higher levels of starch. The higher levels of starch at dusk were determined to be in response to the higher respiration rates occurring at night and the plant adjusting its needs accordingly. Sink organs also are affected by the higher temperatures as sucrose transport is affected. As night temperatures increased to 25ºC, the rate of sucrose transport into bolls increased. This increased rate of sucrose transport led to more rapid influx during early boll development; however, chronic high temperatures led to a decrease in sucrose concentrations compared to the controls within 15 days. (Conner et al., 1972). Additionally, Conner et al. (1972) discovered that warmer night temperatures also hastened days until maximum fiber length, decreasing from near 40 days at 10ºC to 26 days at 20ºC.

EFFECTS OF LOW TEMPERATURES DURING THE DAY

Research concerning low daily temperatures and the diurnal cycle are extremely limited in cotton, which is disconcerting as cotton seedlings may be exposed to suboptimal temperatures regularly in the field. However, the impacts that chilling temperatures have on plants has been investigated for near 100 years (Faris, 1926). As described in the review by Kratsch and Wise (2000), chloroplasts are the most severely impacted organelle compared to other organelles. Under high light, low temperature conditions, starch granules are rapidly depleted, chloroplasts swell, and thylakoids dilate leading to grana dissimilation for chronic conditions (Taylor and Craig, 1971).

In cotton, plants exposed to only 35 minutes of a light intensity of 1700 μmol m^{-2} s^{-1} at 5ºC could only recover 25% of their photosynthetic capacity when returned to optimal temperatures (Payton et al., 2001). It is generally recognized that lower temperatures reduce enzymatic reaction rates which limit the capacity for CO_2 fixation and photorespiration (Huner et al., 1998). Colder temperatures further increase the potential for reactive oxygen species produced due to an inability to utilize incoming light energies for photosynthesis that are then shunted to O_2 photoreduction (Wise and Naylor, 1987). Primarily, excess energies are diverted into the xanthophyll cycle where the excess energy is subsequently converted to heat and removed primarily via transpiration or convection (Demmig-Adams and Adams, 1996). As reviewed by Aro et al. (1993), particularly subject to oxidative damage is the D1 protein of the D1-D2 heterodimer centrally located in the PSII complex. Additionally, colder temperatures limit membrane lipid movement and reduce the capacity for damaged D1

degradation by proteinases by decreasing the enzymatic turnover rate (Huner et al., 1998). Transgenic cotton with increased antioxidant levels of stromal superoxide dismutase, ascorbate peroxidase, and glutathione reductase provided increased protection of the PSII complex under cooler temperatures by facilitating electron transfer further downstream of PS II (Kornyeyev et al., 2001). Therefore, increased antioxidant pools may assist in the photosynthetic rebound of the chloroplast following cold, high light stress (Kornyeyev, 2003).

Cold temperatures also decrease reaction rates within the cell. Sucrose phosphate synthase (SPS) is regarded as the regulator of sucrose synthesis particularly under low temperatures where increased levels of sucrose are linked to increased levels of SPS activity (Winter and Huber, 2000). However, leaf sucrose concentrations in cotton increase due to alterations in the enzymology of sucrose metabolism under low temperatures, suggesting that SPS is not as affected by cooler temperatures as other metabolic enzymes (Guy et al., 1992). For instance, starch synthesis under cold temperatures is impacted by the reduction in the amount of precursors required for synthesis by negatively affecting both carbon fixation and fructose-2,6-biphosphate regulatory mechanisms (Stitt et al., 1988). Respiration decreases at a greater extent than carbon assimilation, thus the inorganic phosphates needed for photophosphorylation which are made available by respiration are reduced further hindering photosynthetic capacities (Paul and Foyer, 2001; Stitt et al., 1988).

It has been observed that under high light, colder conditions, excess sucrose and other sugar intermediates not used for respiration can be cannibalized for necessary photosynthetic intermediates and phosphates (Pollock and Lloyd, 1987). However, when Königer and Winter (1993) examined cotton leaves under high light intensities at 20ºC, they identified a significant decrease in net photosynthetic rates that persisted for as long as temperatures were kept cool. Interestingly, the total carbohydrates in the colder leaves remained identical to those of the control. At the end of the light period, concentrations of soluble carbohydrates in the cooler leaves were greater than the control, but at the end of the night period, the inverse was true. The insoluble carbohydrate concentration remained statistically similar over the course of the experiment. Also identified was a possible feedback inhibition, where excess carbohydrate could initiate a decline of photosynthetic rates. Earlier results from Goldschmidt and Huber (1992) indicated that neither sucrose nor its photosynthetic intermediates inhibit photosynthesis; however, these results did not consider cold daytime temperatures, which may be an overriding factor. Later work identified that sucrose accumulation represses the expression of the sucrose symporter necessary for phloem translocation (Chiou and Bush, 1998) and activates other carbohydrate-sensitive enzymes involved in sucrose and starch regulation and metabolism (Koch, 2004).

EFFECTS OF HIGH TEMPERATURES DURING THE DAY

The effects of heat on the photosynthetic apparatus are extensively addressed in the literature across many plant species, including cotton, and indicate a strong negative correlation between increasing temperatures and carbon assimilation (Chaitanya et al., 2001; Cornish et al., 1991; Pastenes and Horton, 1996; Sharkey, 2005; Timlin et al., 2006). Thus, any effect of high temperatures on the photosynthetic apparatus will have a direct impact on the diurnal production and use of starch and sucrose export.

For many years, PSII has been categorized as being the most heat-sensitive component of the photosynthetic apparatus (Berry et al., 1980). Recent work indicates that other factors may cloud the simplicity of Berry's initial analysis, as PSII is more robust than previously thought. For example, it was determined by Gombos et al. (1994) that lasting negative effects on the PSII apparatus rarely occur until temperatures exceed 45ºC. Additionally, negative effects of high temperature may be compensated by the currently increasing atmospheric CO_2 concentrations. Previous work has shown that cotton grown under increased CO_2 and higher temperatures had greater leaf area, increased photosynthetic capacity, and a higher boll retention when compared to normal CO_2 and higher temperatures (Mauney et al., 1994; Radin et al., 1987; Reddy et al., 1998). Further work in soybean by Vu et al. (2001) showed that at CO_2 concentrations near 700 ppm the photosynthetic capacity could be maintained with minimal damage to carbohydrate manufacture even when temperatures exceeded 45ºC. At these higher temperatures, the test plants were still able to store starch in significantly greater amounts and have higher soluble sugar concentrations at both predawn and pre-dusk hours than the control plants. Work performed by Reddy et al. (1998) indicated

that cotton was especially sensitive to increased CO_2 levels for increased photosynthetic rates during photosynthesis. At CO_2 concentrations of 450 ppm, cotton maintained significantly higher rates of photosynthesis at moderate temperature stress of 36°C with no reduction in rubisco activase activity.

Research by Crafts-Brandner and Salvucci (2000) suggested that rubisco was not the limiting factor in photosynthetic decline under high temperature stress. Isolated rubisco from cotton leaves failed to decrease activity until temperatures exceeded 50°C, far outside normal growing conditions. In contrast, the rate for its isolated activase was limited at 42°C. Thus, the upper maximum temperature limit for photosynthetic capacity is limited by activase and not rubisco itself.

Additionally, heat stress can increase the permeability of the thylakoid membrane due to increased amounts of lipid peroxidation (Bukhov et al., 1999; Xu et al., 2010). The disruption of membrane integrity results in an interference of thylakoid reactions, including photosynthesis (Schrader et al., 2004). Additionally, the porous membrane loses the ability to maintain proper thylakoid proton gradients, limiting ATP production from PSII (Allen, 2003; Bukhov et al., 1999) . To compensate for the decrease in ATP, electron flow is increased to the cyclic photophosphorylation pathway of PSI (Bukhov and Carpentier, 2004; Bukhov et al., 2001). This allows for carbon assimilation to continue by providing intermediates during photorespiration and subsequent starch breakdown (Weise et al., 2006).

However, heat stress also increases the amount of reactive oxygen species present within the cell (Allakhverdiev et al., 2008), which must be reduced to avoid photoinhibition. Two of the largest pathways to assist in the maintenance of the PSII complex include the regulation of photosynthetic reactions through the redox mediation of the plastoquinone pool, and the xanthophyll regulatory pathways. Described by Mubarakshina and Ivanov (2010), the plastoquinone pool performs a dual role in reactive oxygen species regulation. First, it is able to reduce oxygen to a superoxide by plastosemiquinone. Second, it can transform superoxide into hydrogen peroxide by plastohydroquinone. This hydrogen peroxide can then be utilized as a signal molecule for gene expression (Gechev et al., 2002), or as a protectant from both photoinhibition and photooxidation (Karpinski et al., 1999). In the xanthophyll cycle, the conversion of violaxanthin to zeaxanthin is responsible for the photo-protection of photosynthesis by dissipating excess light energy from chlorophyll into heat energy to protect PSII (Müller et al., 2001). Additionally, zeaxanthin is capable of stabilizing thylakoid membranes by functioning as an antioxidant (Havaux et al., 2007). Yin et al (2010) also concluded that the xanthophyll pathway plays an important role in mitigating reactive oxygen species from the chloroplast. Nonetheless, continued stress led to an accumulation of reactive oxygen species, due to depletion of antioxidant pools.

Likewise, heat stress can have negative impacts upon sucrose related enzyme activities. Work in tomatoes (*Solanum lycopersicum* L.) indicated that heat shocked fruit embryos had significantly decreased sucrose synthase activities (Wang et al., 1993). This reduction in sucrose synthase activity can lead to an increase in sucrose concentration within the developing pericarp. This excess sucrose can reduce the gradient between source and sink, reducing phloem flow to the developing ovary (Walker et al., 1978). Increased sucrose concentrations within the developing boll has been known to cause ovary swelling, fruit deformities, and increased rates of abscission in cotton (Darnell, 2013). Increased temperatures also affect respiration rates within the cotton ovule. The optimal temperature for cellulose synthesis is approximately 28°C and temperatures above this reduce cellulose deposition and substantially increase respiration rates, reducing fiber elongation (Roberts et al., 1992).

FINAL THOUGHTS

The diurnal fluctuations of carbon from its assimilation in the leaves, its export into the phloem, and its use in sink tissues has been studied in its individual parts for quite some time. However, studies relating temperature to the diurnal effects in cotton have been scarce. Some temperature profiles, such as maximum temperatures during the day have had extensive research invested. This is understandable because a majority of cotton within the United States is flowering in mid-summer when high temperatures occur. However, other temperature profiles have been studied in far less detail, such as the influence high night temperature stress has upon subsequent sucrose flux. This diurnal examination is especially important in cotton, where modern cultivars are presented with a constricted bottleneck of genetic stock to derive more desirable traits (Iqbal et al.,

2001). The general diurnal summary presented here is a synthesis of investigations from many different species, due in large part to the dearth of information for a particular temperature profile related to cotton. It does not appear that the diurnal import and export of sucrose has been studied in any great significance for more than a quarter century since Hendrix (1986). Given the increase in genetic engineering to maximize particular traits, it is only prudent for research to reexamine the diurnal sucrose cycle and maximize its capability on a whole plant level.

REFERENCES

Allakhverdiev, S.I., V.D. Kreslavski, V. V Klimov, D. a Los, R. Carpentier, and P. Mohanty. 2008. Heat stress: an overview of molecular responses in photosynthesis. Photosynth. Res. 98(1-3): 541–550.

Allen, J.F. 2003. Cyclic, pseudocyclic and noncyclic photophosphorylation: New links in the chain. Trends Plant Sci. 8(1): 15–19.

Allen, D.J., and D.R. Ort. 2001. Impacts of chilling temperatures on photosynthesis in warm-climate plants. Trends Plant Sci. 6(1): 36–42.

Aro, E.M., I. Virgin, and B. Andersson. 1993. Photoinhibition of Photosystem II. Inactivation, protein damage and turnover. BBA - Bioenerg. 1143(2): 113–134.

Ashley, D. 1972. 14C-labelled photosynthate translocation and utilization in cotton plants. Crop Sci. 12(1): 69–74.

Berry, J., O. Björkman, and O. Bjorkman. 1980. Photosynthetic response and adaptation to temperature in higher plants. Annu. Rev. Plant Physiol. 31(1): 491–543.

Bibi, A.C., D.M. Oosterhuis, and E.D. Gonias. 2008. Photosynthesis, quantum yield of Photosystem II and membrane leakage as affected by high temperatures in cotton genotypes. J. Cotton Sci. 12: 150–159.

Boykin, D.L., R.R. Carle, C.D. Ranney, and R. Shanklin. 1995. Weather data summary for 1964-1993 Stoneville, MS. Tech. Bull. 201 Mississippi Agric. For. Exp. Station. Mississippi State.

Bukhov, N., and R. Carpentier. 2004. Alternative photosystem I-driven electron transport routes: Mechanisms and functions. Photosynth. Res. 82(1): 17–33.

Bukhov, N.G., G. Samson, and R. Carpentier. 2001. Non-photosynthetic reduction of the intersystem electron transport chain of chloroplasts following heat stress. The pool size of stromal reductants. Photochem. Photobiol. 74(3): 438–43.

Bukhov, N.G., C. Wiese, S. Neimanis, and U. Heber. 1999. Heat sensitivity of chloroplasts and leaves: Leakage of protons from thylakoids and reversible activation of cyclic electron transport. Photosynth. Res. 59(1): 81–93.

Burke, J.J., J.R. Mahan, and J.L. Hatfield. 1988. Crop-specific thermal kinetic windows in relation to wheat and cotton biomass production. Agron. J. 80(4): 553–556.

Carmo-Silva, A.E., and M.E. Salvucci. 2011. The activity of Rubisco's molecular chaperone, Rubisco activase, in leaf extracts. Photosynth. Res. 108(2-3): 143–55.

Chaitanya, K.V., D. Sundar, and A.R. Reddy. 2001. Mulberry leaf metabolism under high temperature stress. Plant Sci. 44(3): 379–384.

Chang, C.W. 1979. Starch and its component ratio in developing cotton leaves. Plant Physiol. 63(5): 973–977.

Chiou, T.J., and D.R. Bush. 1998. Sucrose is a signal molecule in assimilate partitioning. Proc. Natl. Acad. Sci. U. S. A. 95(8): 4784–4788.

Conner, J.W., D.R. Krieg, and J.R. Gipson. 1972. Accumulation of simple sugars in developing cotton bolls as influenced by night temperatures. Crop Sci. 12: 752.

Constable, G., and H. Rawson. 1980. Effect of leaf position, expansion and age on photosynthesis, transpiration and water use efficiency of cotton. Aust. J. Plant Physiol. 7(1): 89.

Cornish, K., J.W. Radin, E.L. Turcotte, Z. Lu, and E. Zeiger. 1991. Enhanced photosynthesis and stomatal conductance of pima cotton (*Gossypium barbadense* L.) Bred for Increased Yield. Plant Physiol. 97(2): 484–489.

Crafts-Brandner, S.J., and M.E. Salvucci. 2000. Rubisco activase constrains the photosynthetic potential of leaves at high temperature and CO_2. Proc. Natl. Acad. Sci. U. S. A. 97(24): 13430–13435.

Darnell, R. 2013. Night temperature and source-sink effects on growth, leaf carbon exchange rate, and carbohydrate accumulation in bell pepper ovaries. J. Am. Soc. Hortic. Sci. 138(5): 331–337.

Demmig-Adams, B., and W.W. Adams. 1996. The role of xanthophyll cycle carotenoids in the protection of photosynthesis. Trends Plant Sci. 1(1): 21–26.

Faris, J.A. 1926. Cold chlorosis of sugar cane. p. 885–891. *In* Phytopathology.

Feild, T.S., L. Nedbal, and D.R. Ort. 1998. Nonphotochemical reduction of the plastoquinone pool in sunflower leaves originates from chlororespiration. Plant Physiol. 116(4): 1209–1218.

Frantz, J.M., N.N. Cometti, and B. Bugbee. 2004. Night temperature has a minimal effect on respiration and growth in rapidly growing plants. Ann. Bot. 94(1): 155–166.

Gamalei, Y. V, A.J.E. Van Bel, M. V Pakhomova, and A. V Sjutkina. 1994. Planta minor-vein configuration. : 443–453.

Gechev, T., I. Gadjev, F. Van Breusegem, D. Inzé, S. Dukiandjiev, V. Toneva, and I. Minkov. 2002. Hydrogen peroxide protects tobacco from oxidative stress by inducing a set of antioxidant enzymes. Cell. Mol. Life Sci. 59(4): 708–714.

Gibon, Y., O.E. Bläsing, N. Palacios-Rojas, D. Pankovic, J.H.M. Hendriks, J. Fisahn, M. Höhne, M. Günther, and M. Stitt. 2004. Adjustment of diurnal starch turnover to short days: Depletion of sugar during the night leads to a temporary inhibition of carbohydrate utilization, accumulation of sugars and post-translational activation of ADP-glucose pyrophosphorylase in the followin. Plant J. 39(6): 847–862.

Goldschmidt, E.E., and S.C. Huber. 1992. Regulation of photosynthesis by end-product accumulation in leaves of plants storing starch, sucrose, and hexose sugars. Plant Physiol. 99(4): 1443–8.

Gombos, Z., H. Wada, E. Hideg, and N. Murata. 1994. The unsaturation of membrane lipids stabilizes photosynthesis against heat stress. Plant Physiol. 104(2): 563 –567.

Graf, A., and A.M. Smith. 2011. Starch and the clock: The dark side of plant productivity. Trends Plant Sci. 16(3): 169–175.

Granot, D., G. Kelly, O. Stein, and R. David-Schwartz. 2014. Substantial roles of hexokinase and fructokinase in the effects of sugars on plant physiology and development. J. Exp. Bot. 65(3): 809–19.

Guinn, G. 1982. Causes of square and boll shedding. USDA Tech. Bull. 1672: 1–21.

Guy, C.L., J.L. Huber, and S.C. Huber. 1992. Sucrose phosphate synthase and sucrose accumulation at low temperature. Plant Physiol. 100(1): 502–508.

Havaux, M., L. Dall'Osto, and R. Bassi. 2007. Zeaxanthin has enhanced antioxidant capacity with respect to all other xanthophylls in arabidopsis leaves and functions independent of binding to PSII antennae. Plant Physiol. 145(4): 1506–1520.

Van Heerden, P.D.R., G.H.J. Krüger, J.E. Loveland, M. a J. Parry, and C.H. Foyer. 2003. Dark chilling imposes metabolic restrictions on photosynthesis in soybean. Plant, Cell Environ. 26(2): 323–337.

Hendrix, D.L., and R.I. Grange. 1991. Carbon partitioning and export from mature cotton leaves. Plant Physiol. 95: 228–233.

Hendrix, D.L., and S.C. Huber. 1986. Diurnal fluctuations in cotton leaf carbon export, carbohydrate content, and sucrose synthesizing enzymes. Plant Physiol. 81(2): 584–586.

Hesketh, J.D., D.N. Baker, and W.G. Duncan. 1972. Simulation of growth and yield in cotton: iii. environmental control of morphogenesis. Crop Sci. 12(4): 436.

Hewitt, J.D., L.L. Casey, and R.W. Zobel. 1985. Effect of day length and night temperature on starch accumulation and degradation in soybean. Ann. Bot. 56(4): 513–522.

Huber, S.C., and J.L. Huber. 1996. Role and regulation of sucrose-phosphate synthase in higher plants. Annu. Rev. Plant Physiol. Plant Mol. Biol. 47(1): 431–444.

Hummel, M., F. Rahmani, S. Smeekens, and J. Hanson. 2009. Sucrose-mediated translational control. Ann. Bot. 104: 1–7.

Huner, N.P. a, G. Öquist, and F. Sarhan. 1998. Energy balance and acclimation to light and cold. Trends Plant Sci. 3(6): 224–230.

Iqbal, M.J., O.U.K. Reddy, K.M. El-Zik, and a. E. Pepper. 2001. A genetic bottleneck in the 'evolution under domestication' of upland cotton *Gossypium hirsutum* L. examined using DNA fingerprinting. TAG Theor. Appl. Genet. 103(4): 547–554.

Karpinski, S., H. Reynolds, B. Karpinska, G. Wingsle, G. Creissen, and P. Mullineaux. 1999. Systemic signaling and acclimation in response to excess excitation energy in Arabidopsis. Science 284(5414): 654–657.

Koch, K. 2004. Sucrose metabolism: regulatory mechanisms and pivotal roles in sugar sensing and plant development. Curr. Opin. Plant Biol. 7(3): 235–46.

Königer, M., and K. Winter. 1993. Reduction of photosynthesis in sun leaves of *Gossypium hirsutum* L. under conditions of high light intensities and suboptimal leaf temperatures. Agronomie 13(7): 659–668.

Kornyeyev, D. 2003. Effect of chloroplastic overproduction of ascorbate peroxidase on photosynthesis and photoprotection in cotton leaves subjected to low temperature photoinhibition. Plant Sci. 165(5): 1033–1041.

Kornyeyev, D., B. a. Logan, P. Payton, R.D. Allen, and a. S. Holaday. 2001. Enhanced photochemical light utilization and decreased chilling-induced photoinhibition of photosystem II in cotton overexpressing genes encoding chloroplast-targeted antioxidant enzymes. Physiol. Plant. 113(3): 323–331.

Kratsch, H.A., and R.R. Wise. 2000. The ultrastructure of chilling stress. Plant, Cell Environ. 23(4): 337–350.

Krause, G.H., and E. Weis. 1991. Chlorophyll fluorescence and photosynthesis: the basics. Annu. Rev. Plant Physiol. Plant Mol. Biol. 42(1): 313–349.

Lawrence, C., and A.S.S. Holaday. 2000. Effects of mild night chilling on respiration of expanding cotton leaves. Plant Sci. 157(2): 233–244.

Loka, D.A., and D.M. Oosterhuis. 2010. Effect of high night temperatures on cotton respiration, ATP levels and carbohydrate content. Environ. Exp. Bot. 68(3): 258–263.

Lu, Y., and T.D. Sharkey. 2006. The importance of maltose in transitory starch breakdown. Plant, Cell Environ. 29(3): 353–366.

Lunn, J.E., R. Feil, J.H.M. Hendriks, Y. Gibon, R. Morcuende, D. Osuna, W.-R. Scheible, P. Carillo, M.-R. Hajirezaei, and M. Stitt. 2006. Sugar-induced increases in trehalose 6-phosphate are correlated with redox activation of ADPglucose pyrophosphorylase and higher rates of starch synthesis in Arabidopsis thaliana. Biochem. J. 397: 139–148.

Marutani, Y., Y. Yamauchi, Y. Kimura, M. Mizutani, and Y. Sugimoto. 2012. Damage to photosystem II due to heat stress without light-driven electron flow: Involvement of enhanced introduction of reducing power into thylakoid membranes. Planta 236(2): 753–761.

Mauney, J., B. Kimball, P. Pinterjr, R. Lamorte, K. Lewin, J. Nagy, and G. Hendrey. 1994. Growth and yield of cotton in response to a free-air carbon dioxide enrichment (FACE) environment. Agric. For. Meteorol. 70(1-4): 49–67.

Mubarakshina, M.M., and B.N. Ivanov. 2010. The production and scavenging of reactive oxygen species in the plastoquinone pool of chloroplast thylakoid membranes. Physiol. Plant. 140(2): 103–110.

Müller, P., X.P. Li, and K.K. Niyogi. 2001. Non-photochemical quenching. A response to excess light energy. Plant Physiol. 125(4): 1558–1566.

Mutsaers, H.J.W. 1976. Growth and assimilate conversion of cotton bolls (*Gossypium hirsutum* L.). 2. Influence of temperature on boll maturation period and assimilate conversion. Ann. Bot. 40(2): 317–324.

Pastenes, C., and P. Horton. 1996. Effect of high temperature on photosynthesis in beans (I. Oxygen evolution and chlorophyll fluorescence). Plant Physiol. 112(3): 1245.

Paul, M.J., and C.H. Foyer. 2001. Sink regulation of photosynthesis. J. Exp. Bot. 52(360): 1383–1400.

Payton, P., R. Webb, D. Kornyeyev, R. Allen, and A.S. Holaday. 2001. Protecting cotton photosynthesis during moderate chilling at high light intensity by increasing chloroplastic antioxidant enzyme activity. J. Exp. Bot. 52(365): 2345–2354.

Pollock, C.J., and E.J. Lloyd. 1987. The Effect of Low Temperature upon Starch, Sucrose and Fructan Synthesis in Leaves. Ann. Bot. 60: 231–235.

Radin, J.W., B. a. Kimball, D.L. Hendrix, and J.R. Mauney. 1987. Photosynthesis of cotton plants exposed to elevated levels of carbon dioxide in the field. Photosynth. Res. 12(3): 191–203.

Reddy, V.R., K.R. Reddy, and D.N. Baker. 1991. Temperature effect on growth and development of cotton during the fruiting period. Agron. J. 83(1): 211–217.

Reddy, K.R., V.R. Reddy, and H.F. Hodges. 1992. Temperature effects on early season cotton growth and development. Agron. J. 84(2): 229–237.

Reddy, A.R., K.R. Reddy, and H.F. Hodges. 1998. Interactive effects of elevated carbon dioxide and growth temperature on photosynthesis in cotton leaves. Plant Growth Regul. 26: 33–40.

Roberts, E.M., N.R. Rao, J.Y. Huang, N.L. Trolinder, and C.H. Haigler. 1992. Effects of cycling temperatures on fiber metabolism in cultured cotton ovules. Plant Physiol. 100(2): 979–986.

Schrader, S.M., R.R. Wise, W.F. Wacholtz, D.R. Ort, and T.D. Sharkey. 2004. Thylakoid membrane responses to moderately high leaf temperature in Pima cotton. Plant, Cell Environ. 27(6): 725–735.

Servaites, J.C. 1990. Inhibition of ribulose 1,5-bisphosphate carboxylase/oxygenase by 2-carboxyarabinitol-1-phosphate. Plant Physiol. 92(4): 867–870.

Sharkey, T.D. 2005. Effects of moderate heat stress on photosynthesis: importance of thylakoid reactions, rubisco deactivation, reactive oxygen species, and thermotolerance provided by isoprene. Plant, Cell Environ. 28(3): 269–277.

Singh, B., L. Haley, J. Nightengale, H.K. Won, C.H. Haigler, and a. S. Holaday. 2005. Long-term night chilling of cotton (*Gossypium hirsutum*) does not result in reduced CO2 assimilation. Funct. Plant Biol. 32(7): 655–666.

Smith, A.M., and M. Stitt. 2007. Coordination of carbon supply and plant growth. Plant, Cell Environ. 30(9): 1126–1149.

Snider, J.L., D.M. Oosterhuis, B.W. Skulman, and E.M. Kawakami. 2009. Heat stress-induced limitations to reproductive success in *Gossypium hirsutum*. Physiol. Plant. 137(2): 125–138.

Stewart, J. 1986. Integrated events in the flower and fruit. p. 261–300. *In* Mauney, J., Stewart, J.M. (eds.), Cotton Physiology. The Cotton Foundation, Memphis, TN.

Stitt, M., I. Wilke, R. Feil, and H.W. Heldt. 1988. Coarse control of sucrose-phosphate synthase in leaves: Alterations of the kinetic properties in response to the rate of photosynthesis and the accumulation of sucrose. Planta 174(2): 217–230.

Taylor, A.O., and A.S. Craig. 1971. Plants under climatic stress: II. Low temperature, high light effects on chloroplast ultrastructure. Plant Physiol. 47(5): 719–725.

Timlin, D., S.M. Lutfor Rahman, J. Baker, V.R. Reddy, D. Fleisher, and B. Quebedeaux. 2006. Whole plant photosynthesis, development, and carbon partitioning in potato as a function of temperature. Agron. J. 98(5): 1195–1203.

Usadel, B., O.E. Bläsing, Y. Gibon, K. Retzlaff, M. Höhne, M. Günther, and M. Stitt. 2008. Global transcript levels respond to small changes of the carbon status during progressive exhaustion of carbohydrates in Arabidopsis rosettes. Plant Physiol. 146(4): 1834–1861.

Vu, J.J.C.V., R.W.R. Gesch, A.H.A. Pennanen, L. Allen Hartwell, K.J. Boote, and G. Bowes. 2001. Soybean photosynthesis, Rubisco, and carbohydrate enzymes function at supraoptimal temperatures in elevated CO 2. J. Plant Physiol. 158(3): 295–307.

Walker, A.J., L.C. Ho, and D.A. Baker. 1978. Carbon Translocation in the Tomato: Pathways of Carbon Metabolism in the Fruit. Ann. Bot. 42(4): 901–909.

Walter, A., and U. Schurr. 2005. Dynamics of leaf and root growth: Endogenous control versus environmental impact. Ann. Bot. 95(6): 891–900.

Wang, F., A. Sanz, M.L. Brenner, and A. Smith. 1993. Sucrose synthase, starch accumulation, and tomato fruit sink strength. Plant Physiol. 101(1): 321–327.

Warner, D.A., and J.J. Burke. 1993. Cool night temperatures alter leaf starch and photosystem ii chlorophyll fluorescence in cotton. Agron. J. 85(4): 836-840.

Warner, D.A., A.S. Holaday, and J.J. Burke. 1995. Response of carbon metabolism to night temperature in cotton. Agron. J. 87(6): 1193–1197.

Weise, S.E., S.M. Schrader, K.R. Kleinbeck, and T.D. Sharkey. 2006. Carbon balance and circadian regulation of hydrolytic and phosphorolytic breakdown of transitory starch. Plant Physiol. 141(3): 879–886.

Weise, S.E., A.P.M. Weber, and T.D. Sharkey. 2004. Maltose is the major form of carbon exported from the chloroplast at night. Planta 218(3): 474–482.

Winter, H., and S.C. Huber. 2000. Regulation of sucrose metabolism in higher plants: localization and regulation of activity of key enzymes. Crit. Rev. Biochem. Mol. Biol. 35(4): 253–289.

Wise, R.R., and A.W. Naylor. 1987. Chilling-enhanced photooxidation : The peroxidative destruction of lipids during chilling injury to photosynthesis and ultrastructure. Plant Physiol. 83(2): 272–7.

Wullschleger, S.D., and D.M. Oosterhuis. 1990. Photosynthetic carbon production and use by developing cotton leaves and bolls. Crop Sci. 30(6): 1259–1264.

Xu, Z., G. Zhou, G. Han, and Y. Li. 2010. Photosynthetic potential and its association with lipid peroxidation in response to high temperature at different leaf ages in maize. J. Plant Growth Regul. 30(1): 41–50.

Yin, Y., S. Li, W. Liao, Q. Lu, X. Wen, and C. Lu. 2010. Photosystem II photochemistry, photoinhibition, and the xanthophyll cycle in heat-stressed rice leaves. J. Plant Physiol. 167(12): 959–966.

Zhao, D., K.R. Reddy, V.G. Kakani, S. Koti, and W. Gao. 2005. Physiological causes of cotton fruit abscission under conditions of high temperature and enhanced ultraviolet-B radiation. Physiol. Plant. 124(2): 189–199.