

MOLECULAR BIOLOGY AND PHYSIOLOGY

Cotton Photosynthetic Regulation through Nutrient and Water Availability

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ABSTRACT

Photosynthesis is an extremely complicated process that is fundamental to supporting plant growth. It is regulated by multiple internal and external factors. Three factors regulating photosynthesis over which cotton producers can exert some influence are the levels of potassium, nitrogen, and soil moisture. Research has shown that deficient levels of all three depress canopy photosynthesis and yield through the production of a smaller plant with less leaf area to intercept incoming solar radiation. In addition, leaf photosynthesis is impacted by potassium at both the stomatal and non-stomatal level. Nitrogen is a component of both proteins and chlorophyll molecules and as such impacts leaf photosynthesis through effects on dark and light reaction components of photosynthesis. Stomatal factors are the dominant photosynthetic regulating influence when moisture deficit stress is severe, while non-stomatal factors predominate when the moisture deficit stress is mild. A producer can impact yield and profitability for a given field through efficient use and management of these photosynthetic regulatory inputs.

Photosynthesis is one of the principle physiological processes underpinning plant dry matter production. As such, it is also one of the major factors in determining overall cotton (*Gossypium hirsutum* L.) lint production (Pettigrew and Meredith, 1994). It is a highly complex process with many points of regulation along the pathway. This regulation can occur at the canopy level with light interception and at the leaf or molecular level with processes pertaining to carbon dioxide (CO₂) fixation. Beyond the individual effects of these regulatory aspects, there can also potentially be interactions among these influences. Many of these regulatory factors (i.e. light and temperature) are beyond the ability of

producers to easily manipulate. However, there are some regulatory factors that producers can influence. The levels of essential nutrients and soil moisture availability are examples of two regulatory factors that producers can take steps to partially impact. This review article examines how the levels of two macro-nutrients (potassium (K) and nitrogen (N)) can impact photosynthesis and carbon metabolism, in addition to how moisture deficit stress influences photosynthetic performance.

POTASSIUM

Potassium is considered one of the major essential nutrients, it is the most abundant cation in the plant and is associated with many of the physiological processes supporting plant growth and development. The most prominent feature associated with a potassium deficiency in cotton is a reduction in plant stature (Cassman et al., 1989; Mullins et al., 1994; Pettigrew and Meredith, 1997). A consequence of the reduced plant biomass associated with potassium deficiency is a reduction in leaf area index (LAI) (Pettigrew and Meredith, 1997) and a corresponding reduction in canopy solar radiation interception (Gwathmey and Howard, 1998; Pettigrew, 2003). Fewer and smaller leaves under K⁺ deficient conditions explain the LAI reduction (Huber, 1985). The role that K⁺ plays, serving as an osmoticum for the promotion of cell elongation (Dhindsa et al., 1975), may explain the smaller leaves seen on K⁺ deficient plants. Contrasting with the leaf area reduction is the increase in specific leaf weight (SLW) observed for K⁺ deficient plants (Pettigrew and Meredith, 1997; Pettigrew, 1999). A greater SLW is indicative of a thicker or denser leaf. Although a greater SLW is often associated with an increased CO₂ exchange rate (CER) per unit leaf area (Pettigrew et al., 1993; Pettigrew and Meredith, 1994), under a K⁺ deficiency the rate of photosynthesis per unit leaf area is actually reduced (Longstreth and Nobel, 1980; Bednarz et al., 1998).

Potassium impacts photosynthesis through both stomatal and non-stomatal aspects of photosynthesis. At the stomatal level, regulation of conductance is closely impacted by the leaf K⁺ concentration

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through the reversible flux of K^+ ions into and out of the stomatal guard cells (Fischer, 1968; Fischer and Hsiao, 1968). The influx of K^+ into the guard cell lowers the osmotic potential of the cell causing water to flow into the cell. In response to this inward flow of water, the cell elongates and thereby forces the stomates open. Not surprisingly, insufficient levels of leaf K^+ leads to decreased stomatal conductance (Longstreth and Nobel, 1980; Bednarz et al., 1998). Reduced stomatal conductance restricts the movement of CO_2 and H_2O into and out of the intercellular spaces and thereby can limit the amount of CO_2 available for fixation.

Potassium also impacts the non-stomatal side of photosynthesis, but this regulation is primarily through the effect it has on photophosphorylation rather than carbon assimilation. (Huber, 1985) To maintain efficient conversion of sunlight energy to chemical energy in the photophosphorylation process, a chloroplast inner membrane ATPase functions by pumping protons out of the stroma and into the cytosol while allowing K^+ flux into the stroma (Berkowitz and Peters, 1993). This ATPase needs a sufficient level of K^+ to maintain an optimal and efficient activity level (Shingles and McCarty, 1994). The impact K^+ levels have in regulating the stomatal and non-stomatal components of photosynthesis can change throughout the development of a K^+ deficiency. Stomatal factors were the principle factors reducing photosynthesis early in the onset of a K^+ deficiency, but as the deficiency became more pronounced and severe non-stomatal factors became the predominant factors (Bednarz et al. 1998).

In addition to the reductions in leaf area production and photosynthesis per unit leaf area, a further complication caused by a K^+ deficiency is the reduction in translocation of photoassimilates out of the leaf material to reproductive sinks (Ashley and Goodson, 1972). Translocation is restricted under K^+ deficient conditions in part because phloem loading of sucrose is impaired when K^+ levels are insufficient (Marschner, 1995; Deeken et al., 2002; Gajdanowicz et al., 2011; Oosterhuis et al., 2014). Carbohydrates also tend to accumulate in the leaf material as a result of this restricted assimilate translocation (Bednarz and Oosterhuis, 1999; Pettigrew, 1999; Zhao et al., 2001). The increased SLW observed for leaves from K^+ deficient plants is at least partially explained by the accumulation of carbohydrates in K^+ deficient leaves (Pettigrew and Meredith, 1997; Pettigrew, 1999).

The overall effect of a K^+ deficiency on cotton plants is the production of a smaller plant with less leaf area, leading to the generation of a canopy that intercepts less of the incoming solar radiation. Not only do K^+ deficient plants intercept less solar radiation, they utilize that solar radiation less efficiently because of the reduced photosynthetic rate per unit leaf area caused by K^+ deficiency. In addition, the K^+ deficiency induced restriction of photoassimilate translocation out of the leaves further reduces the overall size of the photoassimilate pool available to support growth. Ultimately, this smaller photoassimilate pool contributes to lint yield reductions and compromises the quality of fiber produced under K^+ deficient conditions (Pettigrew, 2008).

NITROGEN

Nitrogen is another major essential nutrient for plant growth. In plant tissue, N is a structural component of the peptide bonds connecting amino acids together to form proteins, it is a factor constituting the amine terminus of each amino acid, it is a component of the nucleic acids, and is a component of the chlorophyll molecule. Similar to K^+ , a main effect on photosynthesis from a N deficiency is reduction in leaf area expansion rate (Radin and Parker, 1979b; Wullschlegel and Oosterhuis, 1990), final leaf area (Radin and Parker, 1979a), and ultimately the canopy's LAI (Wullschlegel and Oosterhuis, 1990). This means that less light will be intercepted by N deficient canopies (Pettigrew and Zeng, 2014).

Nitrogen deficiencies have been shown to decrease the CO_2 exchange rate (CER) per unit leaf area (Longstreth and Nobel, 1980; Radin and Ackerson, 1981; Reddy et al., 1996). In contrast, Wullschlegel and Oosterhuis (1990) failed to find any leaf CER differences between cotton plants receiving adequate and deficient levels of N fertilization. Bondada et al. (1996) found a strong relationship among lint yield, canopy photosynthesis, and soil N. This N effect on canopy photosynthesis is probably predominately caused by the effect N has on leaf area production and light interception. An N deficiency also impacts photosynthesis through effects on both the dark and light reaction components of photosynthesis, which is not surprising considering that N is a component of both proteins and chlorophyll. For instance, Reddy et al. (1996) demonstrated a close relationship between CER, Rubisco activity, and leaf N concentration. Similarly, Pettigrew et al. (2000) reported that leaves

from older cotton canopies had reduced CER, leaf soluble protein concentration, and reduced Rubisco activity compared to younger canopies. They attributed this result to remobilization of the leaf N out the leaves of the older canopy to support the N needs of the developing boll load. Wells (1988) also reported reduced protein and chlorophyll levels along with lower photosynthesis as the cotton plant reached cutout and the boll-filling period. Nitrogen levels also impact the light reaction phase of photosynthesis through effects on both leaf pigment concentrations and chlorophyll fluorescence. Pettigrew and Zeng (2014) reported that field grown cotton plants in plots receiving 112 kg N ha⁻¹ had approximately 25% greater leaf chlorophyll concentrations than the unfertilized plots. Those same fertilized plots averaged approximately 2% greater leaf chlorophyll variable to maximal fluorescence ratios (Fv/Fm) compared to the unfertilized plots in three out of the four years of the study. The chlorophyll Fv/Fm ratio is an estimate of the maximum quantum efficiency of photosystem II.

Nitrogen deficiency has also been reported to reduce overall stomatal conductance (Radin and Ackerson, 1981; Radin and Parker, 1979b), although there are also studies that did not find an N effect on stomatal conductance (Wullschleger and Oosterhuis, 1990a; Radin et al., 1991). Much of those stomatal effects are tied to the interaction between leaf N levels, leaf water status, and leaf abscisic acid (ABA) levels. Radin et al. (1985) demonstrated in field grown cotton plants that the stomata of N deficient plants close at higher leaf water potentials than N sufficient plants. This trait can convey a slight degree of drought tolerance to N deficient plants.

Because of a similarity of symptoms between N deficiency and moisture deficit stress, Radin and Mauney (1986) proposed what they termed the “nitrogen stress syndrome” to describe this interaction. This syndrome is characterized by three attributes associated with N deficiency in cotton: 1) decreased photosynthesis, 2) decreased hydraulic conductance, and 3) stomatal closure at higher leaf water potentials. The decreased photosynthesis (Longstreth and Nobel, 1980; Radin and Ackerson, 1981; Bondada et al., 1996; Reddy et al., 1996) and stomatal conductance (Radin and Ackerson, 1981; Radin and Parker, 1979b; Radin et al., 1985) have been discussed previously. The decreased hydraulic conductance was reported on plants grown in controlled environments and led to reduced leaf area expansion (Radin and

Parker, 1979b; Wullschleger and Oosterhuis, 1990a) and ultimately to reduced LAI (Radin and Parker, 1979a; Wullschleger and Oosterhuis, 1990a). This decreased hydraulic conductance also caused a buildup of carbohydrates in the leaf material prior to flowering (Eaton and Rigler, 1945; Radin et al., 1978), which was later remobilized during the boll-filling period. Unfortunately, field studies were not able to confirm the decreased hydraulic conductance under N deficiency stress that was reported for the controlled environment studies (Radin et al., 1991; Bauer et al., 2014). Therefore, the effect N deficiency has on hydraulic conductance of field grown cotton plants remains unclear.

The overall growth response from N deficient conditions is the production of smaller cotton plants whose canopy intercepts less of the incoming solar radiation. Restricted leaf area expansion caused by N deficiency, possibly because of reduced hydraulic conductance, contributes to the smaller canopy size. Less photosynthesis occurs per unit leaf area for N deficient plants due to restrictions in both the light and dark reactions phases of the photosynthetic process. These restrictions caused by deficient N conditions in the plant's ability to intercept sunlight and then efficiently use it for photosynthesis, reduces the pool of photoassimilates available for growth and yield production (Pettigrew and Zeng, 2014).

WATER DEFICIT STRESS

When a moisture deficit stress becomes severe enough both photosynthetic performance and growth will be negatively impacted. Similar to K and N deficiencies, moisture deficit stress reduces leaf expansion and overall LAI (Jordan et al., 1970; McMichael and Hesketh, 1982; Turner et al. 1986; Ball et al., 1994; Gerik et al., 1996; Pettigrew, 2004). Again, this smaller overall canopy intercepts less of the incoming solar radiation (Pettigrew, 2004). Moisture deficit stress also increases the SLW of cotton plants (Pettigrew, 2004; Pettigrew and Zeng, 2014).

Leaf photosynthesis is also often reduced in response to moisture deficit stress (Ackerson et al., 1977; Sung and Krieg, 1979; Ackerson and Hebert, 1981; McMichael and Hesketh, 1982; Plaut and Federman, 1991; Ephrath et al., 1993; Pettigrew, 2004). This photosynthetic decline can come about from both stomatal and non-stomatal limitations (McMichael and Hesketh, 1982; Marani et al., 1985; Turner et al., 1986; Genty et al., 1987; Ephrath et al.

1990; Faver et al., 1996; Chastain et al., 2014). Sung and Krieg (1979) also reported reduced translocation of photoassimilates out of the leaf material when the plant is under water-deficit stress.

The stomatal conductance response to moisture deficit stress has been quite inconsistent across the many reports in the literature. These inconsistent responses make it difficult to clearly define the role stomatal conductance plays in regulating the photosynthetic response to water deficit stress. Part of the inconsistency may have to do with whether the studies were conducted with field grown plants or on plants grown in environmentally controlled chambers or greenhouses. Carmi and Shalhevet (1983) demonstrated that cotton growth and yield was reduced when the plants were grown in a finite container size that constrained root volume. For container grown plants in growth chamber or greenhouse conditions, water deficit stress reportedly decreases stomatal conductance (Ackerson and Hebert, 1981; Plaut and Federman, 1991; Ennahli and Earl, 2005). In contrast, water deficit stress has been found to either decrease stomatal conductance (McMicheal and Hesketh, 1982; Ephrath et al., 1990; Ephrath et al., 1993; Wullschlegler and Oosterhuis, 1990b; Kitao and Lei, 2007) or not impact the stomatal conductance of field grown plants (Ackerson and Krieg, 1977; Ackerson et al., 1977). Utilizing field grown plants, Faver et al. (1996) were able to document stomatal conductance as the primary component regulating photosynthesis under severe moisture deficit stress because they found that the reductions in CO_2 -exchange rates (CER) and internal CO_2 concentrations (C_i) paralleled the reductions in stomatal conductance when water stress was severe. Radin (1992) put forth a hypothesis based upon temperature effects on leaf ABA concentrations (Radin et al., 1982) to help explain the discrepancy between the performance of field grown plants and plants grown in pots in greenhouses or growth chambers. Basically, higher temperatures in the field leads to decreased ABA accumulation in the leaves, which in turn makes the stomata less sensitive to fluctuations in carbon (C_i) levels and thereby uncoupled from mesophyll photosynthetic components. Raschke (1975) had previously shown that the ABA effect on stomatal conductance was dependent upon C_i levels and vice versa. Additional evidence supporting the different behavior between growth chamber or greenhouse grown plants compared to field grown cotton is the work of Wise et al. (1992), who reported that water

stress induced patchy stomatal closure in non-acclimated growth chamber grown plants, but not in in field grown plants exposed to moisture deficit stress.

Non-stomatal factors also come into play in regulating the photosynthetic response to water deficit stress, but similar to the stomatal response, these effects can be quite inconsistent. Hutmacher and Krieg (1980) found predominant nonstomatal limitations to photosynthesis for field grown plants under a slowly developing water stress because the stress caused a greater reduction in photosynthesis than in leaf conductance. Ephrath et al. (1993) found both CER and stomatal conductance were reduced while C_i was increased in field grown cotton in response to water stress and concluded that non-stomatal factors were the main photosynthetic limiting factors. Faver et al. (1996) also reported that water deficit stress reduced the initial slope of the assimilation (A): C_i curves, correlated with Rubisco activity, and also reduced the A_{max} , correlated with ribulose 1,5-bisphosphate (RuBP) regeneration, (Farquhar et al., 1980) for field grown cotton. They further concluded that for these field grown plants, non-stomatal factors were the primary components regulating photosynthesis under moderate moisture deficit stress because that level of stress only produced small reductions in both C_i and CER but stomatal conductance was decreased substantially. Massacci et al. (2008) reported increased photosynthetic electron transport for field grown cotton experiencing a moderate water stress due to a higher efficiency of the open PSII reaction centers. They also found increased photorespiration under drought stress, which would divert the excess energy away from the photosynthetic apparatus and thereby minimize the production of damaging reactive oxygen species. Similar increases in photorespiration and also in the ratio of dark respiration to gross photosynthesis for drought stressed field grown cotton were reported by Chastain et al. (2014). Kitao and Lei (2007) also reported higher electron transport rates for field grown cotton plants exposed to long term drought conditions and speculated that it could be associated with greater photorespiration under drought stress conditions. Zhang et al (2011) found that drought stressed field grown cotton plants exhibited a greater PS II quantum yield than the non-stressed cotton. In contrast, Inamullah and Isoda (2005) and Ennahli and Earl (2005) reported the moisture deficit stress decreased quantum efficiency for PSII for cotton plants grown in pots in greenhouses. In addition, both Chastain et al. (2014) and

Snider et al. (2014) did not find any effect of drought stress on PS II quantum yields compared to that of non-stressed field grown cotton. Therefore, the effect that drought stress has on PS II quantum yield remains unclear due to the inconsistency of results across the multitude of research reports. Nonetheless, both components of the light and dark reaction phases of photosynthesis have been reported to be impacted by moisture deficit stress and contribute to a non-stomatal regulation of photosynthesis by moisture stress.

Water deficit stress also comes into play with another photosynthetic phenomenon affecting most crop species known as the afternoon photosynthetic hysteresis effect. This hysteresis is a decline in photosynthesis when measured on the same leaves during afternoon as compared to the morning (Pettigrew et al., 1990). The phenomenon has been documented in both upland, *Gossypium hirsutum* L., (Pettigrew et al., 1990; Pettigrew and Turley, 1998; Pettigrew, 2004) and Pima, *Gossypium barbadense* L., (Cornish et al. 1991) cotton. When comparing eight cotton genotypes grown under dryland or irrigated conditions, Pettigrew (2004) reported that the afternoon photosynthetic decline was greater for plants in the dryland treatment compared to irrigated plants. Dryland leaves went from having a 6% statistically higher leaf CER in the morning than irrigated leaves, due to increased SLW and an increased leaf chlorophyll concentration, to exhibiting a 6% lower leaf CER in the afternoon. The light adapted quantum efficiency of PSII was also 10% lower for dryland leaves in the afternoon compared to irrigated leaves after being 9% greater for the dryland leaves in the morning. Afternoon stomatal conductance for the dryland leaves was lower than that found with irrigated leaves, but no stomatal conductance differences were detected in the morning. In contrast, Massacci et al. (2008) found irrigated plants had greater stomatal conductance than dryland plants in the morning, but in the afternoon similar conductance was observed for the two moisture regimes. However, stomatal conductances for both moisture treatments were lower in the afternoon than they were in the morning. Therefore, the afternoon photosynthetic decline for cotton is real and it appears to be more pronounced for cotton undergoing water deficit stress.

While this afternoon photosynthetic decline unquestionably limits overall photosynthetic production, it also offers an opportunity for research directed toward trying to improve afternoon pho-

tosynthesis. The first step is to understand what factor or factors work to limit photosynthesis in the afternoon. Several hypotheses have been offered with supporting data to help explain the photosynthetic hysteresis phenomenon for a number of plant species. An increasing leaf-to-air vapor pressure deficit during the afternoon could elicit stomatal closure and thereby contribute to the afternoon reduction (Bunce, 1982; 1983; Farquhar et al., 1980; Pettigrew et al., 1990). Higher temperatures in the afternoon could push the leaf temperatures outside of the optimal temperature range for photosynthesis and lead to a photosynthetic reduction (Baldocchi et al., 1981; Perry et al., 1983; Reddy et al., 1991; Snider et al., 2009). Feedback inhibition from the diurnal buildup of leaf carbohydrates during the afternoon might depress the photosynthetic process (Nafziger and Koller, 1976; Mauney et al., 1979; Peet and Kramer, 1980). Exposure to intense solar radiation encountered around solar noon could lead to damage of the photosynthetic apparatus through photoinhibition (Powles, 1984). Similarly, intense light conditions can sometimes produce a “down regulation” of the photosynthetic process where the excess absorbed photons are dissipated as heat rather than damaging the photosynthetic structure (Baker and Ort, 1992). Transient and localized water stress in the leaves could also inhibit photosynthesis more in the afternoon compared to the morning through non-stomatal means (Sharkey, 1984). Any and all of these factors, along with various interaction combinations of these factors, can come into play to reduce the photosynthetic performance during the afternoon. More research is needed to further define all that is going on to produce this afternoon photosynthetic decline and to also investigate possible means to mitigate the process.

The reduced plant structure caused by water deficit stress is similar to that observed for both K⁺ and N deficiency in that overall canopy leaf area is reduced and thereby the ability of the canopy to intercept incoming solar radiation is diminished. Furthermore, the photosynthetic rate for a given leaf area is reduced by water stress through both stomatal and non-stomatal factors. Stomatal factors are the dominant regulating factors under severe moisture deficit stress, while non-stomatal factors predominate when the moisture deficit stress is mild (Faver et al., 1996). This reduction in the total photoassimilate and water supply to support reproductive growth leads to yield and fiber quality reductions.

CONCLUSION

Photosynthesis is a basic physiologic process underpinning growth, development, and yield production. Considerable progress has been made in describing this phenomenon that is tightly regulated by many internal and external influences. This manuscript describes the operation of three of the many factors that can regulate the processes of photosynthesis. Photosynthesis is negatively impacted when levels of K^+ , N, or water become deficient; this can ultimately reduce growth, development, and yield. The obvious tactic for producers to mitigate these possible negative influences is to ensure that high enough levels of each of the inputs are always present, ensuring that none of these factors ever limits maximal photosynthesis. Producers must walk a fine line with the levels of these inputs because too high a level of these inputs can also have negative or toxic consequences. Unfortunately, maximal photosynthesis doesn't always translate into higher yields, as there must also be appropriate partitioning of the photoassimilates produced into reproductive growth rather than vegetative growth. With current high prices for these inputs, producers must judiciously manage the allocation of these inputs to achieve the optimal input use efficiency and a canopy photoassimilate production level that is also appropriately paired with the yield potential and yield goal for each individual field.

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