

COTTON PHYSIOLOGY TODAY

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Mechanics of Cotton Productivity

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This newsletter is about the fundamentals of cotton production. Not those we normally think of such as variety selection, fertilization and pest management, but rather the actual production and distribution of carbohydrates created during photosynthesis. This vital series of physiological steps enables cotton to manufacture and deliver food to developing bolls while sustaining its own survival. The interplay between reproductive and vegetative growth is responsible for bountiful yields and rank growth. Understanding the fundamentals of this system can help you increase lint yields and decrease your production of pulp wood.

Photosynthesis is basic plant physiology. The gap between this subject and commercial cotton production may appear deep and wide. In one sense, it is. There are few, if any, immediately valuable production pointers that will result from this discussion. On the other hand, an introduction to this fundamental aspect of the cotton plant can help build a sound management foundation. We need to appreciate the marvelous detail built into this row crop we raise. By examining that detail, we can distinguish between those parts of the plant that can and cannot be modified by our cultural practices. Some things we can modify. Other things we have to adjust to. For example, we can apply water and fertilizer, but we can't control nighttime temperatures. All of these affect the plant's photosynthesis.

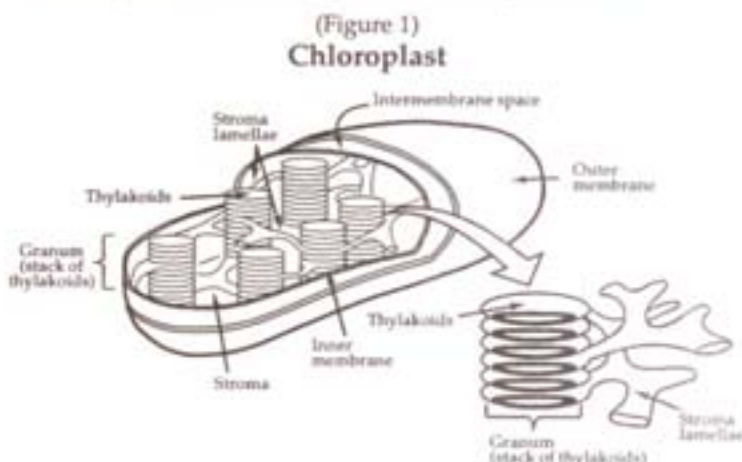
All plant and animal life can be traced to photosynthesis where the sun's radiant energy is captured and transferred to the chemical bonds of sugar molecules. These carbohydrates are then distributed to the different organs of the plant to support continued or future growth. This production and allocation system continues to fascinate plant physiologists seeking to identify and understand its intricacy, complexity and control.

This highly coordinated system is very complex, but highly organized. It can be compared to a factory producing some needed product. Using this analogy, this discussion will focus on the machines making the product, the warehouse that stores the inventory and the distribution network that determines the product's final destination.

Leaf Chloroplasts -- Green Machines

The actual photosynthetic reactions occur in chloroplasts found inside individual leaf mesophyll cells. There are 15-20 chloroplasts per cell. An individual chloroplast consists of an outer double-layered mem-

brane that controls the movement of cellular materials. Inside the chloroplasts a second membrane appears as single strands in some areas and stacked in others (grana). The remainder of the chloroplast is filled with a liquid broth (stroma) of different protein molecules, starch grains and other smaller sub-compartments.



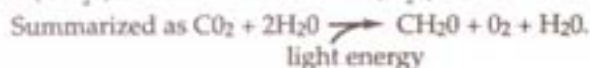
Photosynthesis refers to two coordinated sets of reactions. The light reaction occurs in these grana stacks where the chlorophyll molecules are concentrated. The chlorophyll molecules working in concert serve as antennae to intercept incoming solar radiation of specific frequencies, much like television or radio receivers. When an appropriate wavelength strikes the chlorophyll, an electron is dislodged from the molecule and transferred to a temporary electron carrier molecule (NADPH_2^+). The "hole" left by the displaced electron is filled by an electron donated from water. Energy released in these connected reactions is temporarily stored in the high-energy bonds between phosphate molecules in a second carrier molecule (ATP). The splitting of water, accomplished with the help of many intermediates and manganese, provides electrons to recharge chlorophyll and also produces oxygen for us to breathe.

The second part of photosynthesis, referred to as the dark reactions, utilizes the electron carrier and the energy carrier supplied by the light reactions to incorporate atmospheric carbon dioxide (CO_2) into sugars. The stroma contains the most common protein on earth, an enzyme referred to as RuBisCO. RuBisCO is the enzyme that actually attaches the carbon dioxide onto a sugar molecule, although the entire process involves many enzymes functioning in concert.

The net result of this two phase photosynthetic process is the consumption of two units of

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water (H_2O) and one unit of carbon dioxide (CO_2) to form one unit of oxygen (O_2) from water, one unit of carbohydrate (CH_2O) and one unit of water (H_2O).



Fate of Carbohydrates

Carbohydrates produced during photosynthesis are converted to sucrose for immediate transport to other locations in the plant or stored as starch in the chloroplast. Light, temperature, water, plant growth stage and the location and amount of CH_2O and energy consumers, or sinks, all help determine how much carbohydrate is shipped out immediately and how much is stored. This switching system, which appears to be quite sensitive to the different controlling factors, acts like a traffic light at a busy intersection.

During the day, the chloroplast is capable of producing sugars faster than they can be exported. A substantial portion (20-50%) is converted to starch and stored within the chloroplast. At night, the starch is converted to sucrose for shipment to plant organs that are actively growing, such as bolls, vegetative terminals and roots. When nighttime temperatures fall below 70° , the conversion of starch to sucrose and/or sucrose transport to other organs slow. When the nighttime temperature drops below $55-60^\circ$ the conversion is inhibited and starch remains in the chloroplast the next morning. Nighttime temperatures in the high 70s favor the depletion of stored starch from the chloroplast.

Photosynthetic carbon fixation during the day is associated with the amount of starch stored in the chloroplast. When starch remains in the chloroplast from the night before, less CH_2O is fixed the next day. This would suggest that higher nighttime temperatures would be desirable to allow full photosynthesis during the day.

Photorespiration

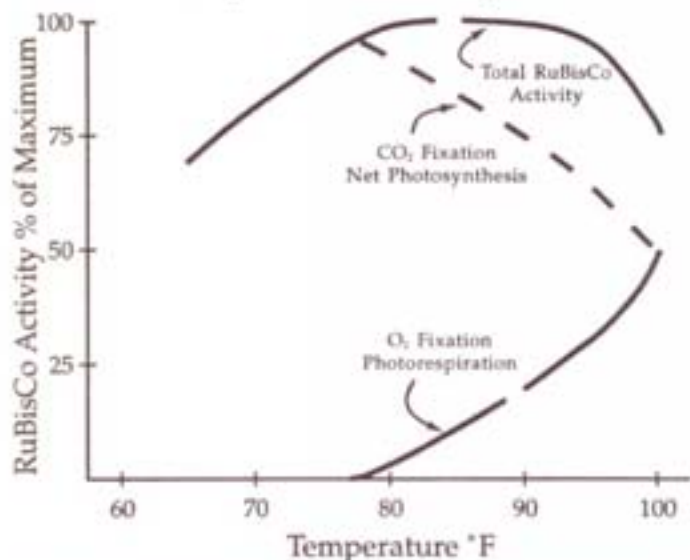
The RuBisCO enzyme is also capable of utilizing oxygen instead of carbon dioxide. When oxygen is used as a reactant, carbon dioxide is released instead of fixed and energy is consumed, a seemingly wasteful process. Photorespiration occurs simultaneously with photosynthesis, which has the effect of reducing the net productivity of the cotton plant (Figure 2).

Photorespiration increases with light intensity and temperature. Temperature is particularly critical in determining the relative concentration of carbon dioxide and oxygen available to RuBisCO. In order for carbon dioxide or oxygen to be used by RuBisCO, they must dissolve in the stroma broth. As temperatures in the stroma increase, the solubility of both gases decreases, but not to the same extent due to the large differences in concentration in the leaf. The ratio of oxygen to carbon dioxide in the stroma increases with temperature, which increases photorespiration. Photorespiration represents

less than 20% of the RuBisCO activity at $75^\circ F$ but is almost 50% when temperatures reach $95^\circ F$.

(Figure 2)

Photorespiration vs. Photosynthesis



Reducing Photorespiration in a Cotton Crop

Some plant species, such as corn and sorghum, referred to as C₄ plants, display little or no photorespiration. Their evolutionary track effectively increased the ratio of carbon dioxide to oxygen at the RuBisCO enzyme site. These species' virtual elimination of photorespiration is partially responsible for the robust growth that characterizes them. Can we or should we eliminate photorespiration in cotton? Probably not.

Photorespiration, while appearing wasteful, also helps to protect cotton from high light intensities and damaging oxygen levels. The products of the light reactions are oxygen and the electron and energy carriers utilized in the dark reactions. When carbon dioxide levels are low because temperatures rise and/or stomata close (reducing gas exchange with the atmosphere), the dark reactions slow, but the light reactions do not. In other words, the two carriers continue to be made as well as oxygen. However, if there are no dark reactions the two carriers cannot unload their cargo and they cannot be recycled for additional duty in the light reactions.

Meanwhile, the radiant energy is still being absorbed by the chlorophyll even though further movement of the electrons has been short circuited. Without the availability of the carriers, the photosynthetic apparatus may be damaged or destroyed by oxygen accepting the electrons producing super oxide (O_2^-), a metabolic monkey wrench. Additionally, high oxygen levels can destroy other parts of the cell. Therefore, photorespiration helps to protect the cotton plant when the dark reactions are unable to keep pace with the light reactions. It should also be noted that photorespiration has not been directly reduced by breeding efforts or through chemical treatment.

Cultural Practices That Reduce Carbohydrate Loss

Is there a practical way to increase the rate of the dark reactions and reduce the loss of carbohydrates? If the levels of atmospheric carbon dioxide continue to increase through our consumption of fossil fuels, the ratio of the two gases will continue to change, reducing photorespiration and increasing net photosynthesis. A more manageable solution can be achieved by optimizing crop water relations so stomata do not close, which modulates chloroplast stroma temperature through evaporative cooling and maintains carbon dioxide levels at the enzymatic site. Irrigation, where available, can be optimized to limit heat stress. Rainfed areas must rely on cultural fundamentals, such as moderate plant populations, full utilization of the rooting zone via subsoiling, or conservation tillage.

Leaf Age and Health

The preceding discussion described the basic mechanics of carbohydrate production within a photosynthetic cell. However, the actual contribution of these cells to overall plant productivity and harvestable yield is determined by the age and health of leaves in which they are located.

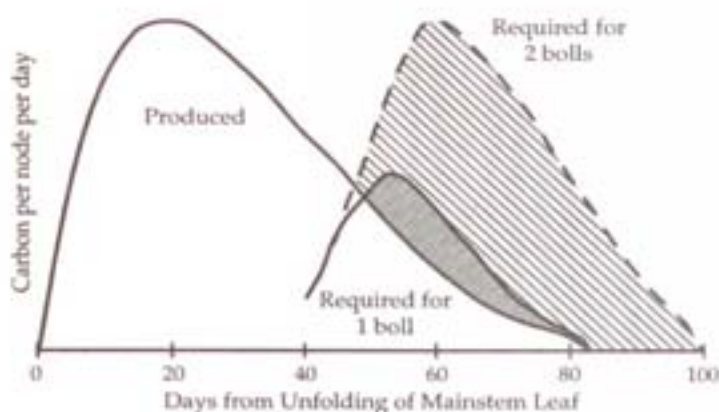
Cotton leaves have a life cycle that begins with initiation in the bud, growth to full size, active middle age, followed by senescence and death. Photosynthesis within the leaf reaches a maximum about 15 days after it unfolds, remains constant for another 20-30 days, then steadily declines for 20 more days, culminating in abscission from the plant. Leaf aging and shading are responsible for this decline. The leaf becomes a net exporter of carbohydrate about 20 days after it unfolds. It remains a net exporter of sugars for other organs until it dies or falls from the plant.

Stress levels within a leaf shorten its life and export capabilities. Water stress will diminish its ability to modulate its internal temperatures causing disruption of its photosynthetic machinery and overall cellular metabolism. Nutrient deficiencies limit the cell's ability to manufacture needed materials for cellular maintenance or export. Disease development also may constrict or occlude the vascular system, in essence clogging the piping used for import and export.

Leaf Productivity and Boll Demands

Research has clearly established that even though leaves are exporting factories of carbohydrate, they may not be sending the supplies when the bolls need them. For example, a mainstem leaf adjacent to a fruiting branch may be 30 to 40 days old before the first position fruit blooms. By this time, the photosynthetic production of that mainstem leaf has begun to decline. One boll growing on the first fruiting branch may need to import more than 75% of its carbohydrate needs from leaves at other nodes. This import demand increases if more than one boll is produced per fruiting branch (Figure 3).

(Figure 3)
Carbohydrate Supply and Demand



Fruit Position

As demands increase from a fruiting branch, some positions take priority. Consider the progression of leaf and fruit development along a given fruiting branch. New leaves and squares are produced on about 8 to 10 day intervals. When the second position fruit blooms, the first position (FP1) boll (if present) is already about 8 days old. That FP1 boll has its greatest increase in demand for imported carbohydrate when about 15 to 25 days old. The FP2 boll (if present) must develop to beyond about 10 days old to insure its retention. Therefore, as the FP1 boll's (already past the crucial 10 day threshold) appetite is increasing the most rapidly, the FP2 is still vulnerable. If there is a deficiency in carbohydrate supply due to shade, water, nutrients, etc., it is the FP2+ positions that are at greatest risk of abortion.

The Resource Pool

So, if bolls on a fruiting branch need to import carbohydrates, where does it come from? First, from the leaves growing closest to it on the same fruiting branch. Other leaves from other nodes and fruiting branches also can contribute, as determined by their age, health and other fruit they support. The cotton plant's carbohydrates not needed for maintenance at the production site then can be considered as part of a reservoir of available supplies.

Where is the pool? As mentioned before, some carbohydrate is retained in the chloroplast as starch grains that can be remobilized as needed. Some carbohydrate is translocated to the roots for later use. The stem itself is full of starch which is drawn on during rapid boll fill. The first 5 to 7 mainstem nodes are major contributors to root growth and starch storage. Photosynthetic production by leaves also may be immediately translocated as sucrose to growing bolls or terminals.

Exported sugars are preferentially translocated downward. This fact has important consequences for cotton growers. If early fruit are lost due to insects or shading, the lower leaves' photosynthetic output that could have helped support those bolls and overall plant

productivity is wasted. Those leaves took time and resources to develop without contributing to the harvestable yield. However, they may support additional root growth that could contribute to increasing the plant's carrying capacity. When the (FP1) boll on a fruiting branch is lost, the FP2 site cannot fully compensate for this loss because the carbon supply from the main stem leaf is less accessible. This helps explain why FP1 sites produce larger and higher quality bolls.

Canopy Photosynthesis

Canopy photosynthesis is a measure of total carbon dioxide use by a section of row. It is a better estimate of potential productivity than measurements of individual leaves because the latter measurement is taken in full sun and uses topmost, fully expanded leaves. Canopy photosynthesis rates comprise the canopy's ability to intercept light and the photosynthetic efficiency of the variety in question. Before canopy closure, canopy photosynthesis and light interception by the canopy is closely related. After canopy closure, however, the relationship is no longer close and is indicative of the inability of the canopy to intercept more light due to complete ground coverage. If the environment is favorable for canopy

development, management schemes which allow greater amounts of light to penetrate into the internal portions of the canopy can be beneficial in terms of yield. Examples of these management schemes are skip rows and narrow rows with lower plant populations.

Wrap-up

The cotton plant's response to its environment is determined by its biological makeup including its photosynthetic machinery and transport mechanisms. Photorespiration, leaf aging, and scheduling problems with carbohydrate supply and demand are all facts. Our challenge is to construct management strategies that recognize biological boundaries, minimize limitations, and take advantage of opportunities.

Cultural practices that accomplish this are:

- Maintain crop moisture status through irrigation, moderate plant populations, subsoiling, conservation tillage, etc.
- Protect early squares and bolls, particularly FP1 positions.
- Insure adequate light penetration into the plant canopy through skip rows, narrow rows, lower plant populations and judicious use of plant regulators.

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