PHYSIOLOGY TODAY

Newsletter of the Cotton Physiology Education Program — NATIONAL COTTON COUNCIL

Technical Services, May 1990

Leaf Physiology and Management

Derrick Oosterhuis, Tom Kerby and Kater Hake

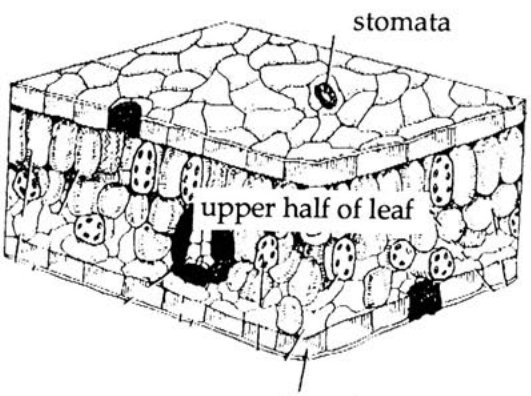
Cotton producers have placed tremendous emphasis on the physiology of fruit development during the last decade. We "plant map" fruit and base management decisions on the number and location of squares and bolls. At the same time, we should not overlook the importance of leaves in crop productivity. Leaves should be thought of as the basic building blocks of cotton production. We need to consider the effect management practices have on both fruit and leaves.

In this issue, we hope to leave you with an understanding of the management decisions that influence leaves and how yield and quality benefit when we sustain healthy young leaves. An associated article in this issue will cover Herbicide Injury to Leaves.

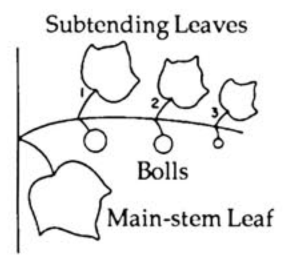
Leaf Structure

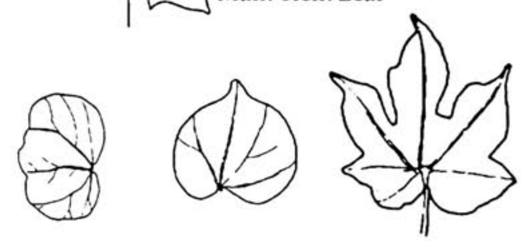
Leaves are an elegant solution to two common plant problems, (1) the need to maximize sunlight absorption to fuel the inefficient light harvesting mechanism of photosynthesis and (2) the need to minimize water loss while maximizing CO_2 uptake. Cotton leaves solve the light harvesting problem by their large flat surfaces and their dense stacking of the light harvesting pigment (chlorophyll) in the upper half of the leaf. Water conservation is achieved by controlling air movement in and out of the leaf through small pores, stomata, located predominately on the lower leaf surface. Since stomata open during the day to allow CO_2 to diffuse into the leaf, unavoidably, water vapor diffuses outward. However, some benefit does derive from this water loss; the plant cools itself during the day to keep leaf temperature below the damaging level of 100°F. Additionally, the flow of water vapor out of the leaf pulls soil water into the root, bringing with it dissolved nutrients such as nitrate.

Leaf Cross Section



Three dominant types of leaves occur on the plant, cotyledons or seed leaves, main-stem leaves and subtending leaves. Cotyledons are mainly storage tissues with minimal photosynthetic capability. Main-stem leaves feed the developing terminal, branches and bolls. While the subtending leaves (those attached to fruiting branches) are critical for boll set and filling.





Leaf Function

The structure of leaves allows them to perform their most critical task, photosynthesis, the capture and storage of light energy. This two-stage process of energy capture and storage allows the plant to fill bolls on bright sunny days and keeps the plant growing at night. Photosynthesis traps light energy in sugar (carbohydrate) molecules, which are used to build the leaf or transported out for growth elsewhere. Cotton leaves that produce carbohydrates in excess of their needs are called "sources", as compared to plant "sinks" that receive nutrients from leaves. "Sinks" can be either bolls, roots or immature stems and leaves. "Sources" on the other hand, are usually leaves. Not all leaves are "sources". In fact, only middle aged leaves are "sources", and capable of supporting boll development. The strongest "source" is a fully illuminated recently expanded leaf, while the strongest "sink" is a 20 to 30

Also In This Issue

day old boll experiencing its most rapid dry weight gain. Bracts and boll walls provide much less photosynthate than leaves.

Even though we seldom hear these terms, successful management practices are directed toward maintaining the balance between "sinks" and "sources". Plant growth regulators, irrigation, and fertilization are used to keep "sources" strong at the same time that the plant builds "sinks" in the form of developing bolls. A management decision that typifies the use of the "source/sink" concept is regrowth control. Whether to control regrowth or let the plant green up and produce new leaves that might help fill late set bolls is a question producers are faced with. Young regrowth will require at least 2 to 3 weeks before the leaves are capable of becoming "sources" by exporting carbohydrates. Additionally before carbohydrate is available to support the initiation of regrowth boll demand or "sinks" must already be low. Clearly, allowing the plant to regrow would be of no benefit for late set bolls and only risks aggrevating insect populations and lint stain.

Leaf Growth

The growth of leaves is largely hidden from the eye. By the time we can see leaves, they're already in the last stage of development and only need to expand. The day after planting, the first true leaf can be seen with a microscope, starting to develop in the shoot tip between the folded cotyledons in the seed, but it takes an additional 3 to 4 weeks before that leaf is visible to the naked eye. In the terminal, cotton leaves develop through cell division, elongation and differentiation into miniature normal shaped leaves that only require expansion to push out into the sunshine. Leaves that develop on fruiting branches form in a similar manner but start from a branch bud. Thrips feed on leaves when they are small and buried in the terminal. For this reason, even minimal thrip feeding can cause a dramatic decrease in leaf area.

Leaf Age and Photosynthesis

Cotton leaves have a limited productive life, just like an athlete, but leaf productivity is measured in days instead of years. For the first 16 days after a leaf begins to unfurl, carbohydrates produced by the photosynthetic machinery are directed towards growth of the new leaf. But as soon as that leaf is near full size (80% expanded), this 16 to 18 day old leaf hits its prime carbohydrate exporting capability. And by the time a leaf is 25 days old, it starts a downhill slide until age 60 to 65 when it no longer exports carbohydrates to fill bolls. During mid-season, the most active main-stem leaf is approximately 5 nodes from the top, while the leaf 13 nodes from the top has already aged to the point where it is non-functional.

One of the most important management factors to derive from leaf aging studies is that maturation of late set bolls requires healthy late season leaves. If we cut short new leaf development, we do not set and mature late bolls. This has been clearly pointed out by plant mapping. Late-set bolls are invariably first position bolls, because when a 1st position square appears in the terminal, 2 young leaves, are also developed, the main-stem leaf and that squares subtending leaf. Other positions on the fruiting branch only come with 1 new leaf, the subtending leaf. Thus by its very nature, first position squares have a greater "source" of new young leaves for boll filling even if the terminal does not produce another leaf above.

Many plant researchers have sought an illusive enhancement in photosynthetic efficiency, or "source" strength, because crops only capture a small percent of the light energy they receive. The most efficient crop plants, which include corn and sorghum, can trap 3.5% of the light energy. Cotton by comparison only traps 1.3% of the light energy. Although we have not been able to increase photosynthesis other than to enrich the air around the crop with CO_2, we can avoid decreasing photosynthesis or "source" strength by maintaining healthy young non-stressed leaves.

Leaf Contribution to Early Vegetative Growth

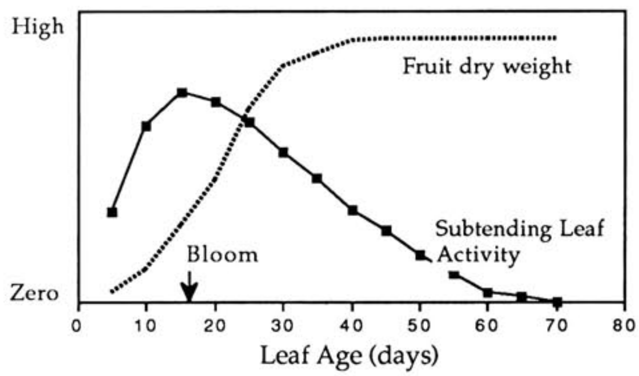
Prior to squaring, the only leaves on the plant are main-stem leaves and cotyledons. These are directly linked with the main-stem and thus feed the developing shoot tip and root system. Loss of both cotyledons within the first week after emergence severely delays maturity, because these storage organs have not had time to transfer out their stored nutrients. Young cotyledons are also a source of photosynthetic carbohydrate. Damage to older cotyledons or early main-stem leaves is less detrimental because the growing points limit plant development and not leaf area or stored nutrients. In fact, prior to squaring, healthy leaves generally produce more carbohydrates than the plant needs. They store the rest as starch or protein. Once the plant develops more "sinks" (fruit, branches, and roots) and the temperature warms, the plant can utilize the carbohydrate produced from a larger leaf area. In short season production systems, the tolerance to early leaf damage is less, because a slight delay in maturity from early leaf damage often results in lost yield. Once bolls are set on the plant, leaf damage is of greater concern regardless of the growing season, because boll growth is often limited by the ability of leaves to fill them and any additional stress to the leaves can decrease yield. The table below displays the relative yield sensitivity of leaves to damage for a short and long growing season.

Sensitivity to Leaf Damage

	Cotyledon	Pre-square	Squaring	Bloom	Boll Opening
Short Season	High	Moderate	Mod-high	High	Low
Long Season	High	Low	Moderate	High	Low

Leaf Contribution to Boll Filling

Cotton plants are perennial in nature and designed to grow for 10 years, not just one. Like any other shrub, they readily build leaves, stem and roots, but are inefficient at building fruit. Many of our management practices and breeding efforts have been aimed at encouraging the plant to partition more carbohydrate into bolls and less into vegetation. These management practices attempt to overcome several deficiencies in the way cotton grows. Squares can support themselves with carbohydrates from the bracts, but once a boll reaches 10 days old it has a voracious appetite for mineral nutrients and carbohydrates. The young boll derives most of its food from the subtending leaf. If this leaf is shaded, for example due to cloudy weather or dense growth, this young 4 to 7-day old boll will shed. The following figure shows a fruits weight gain and it's subtending leaf's photosynthetic capacity during their development.



(Wullschleger and Oosterhuis, 1990)

Research in California and Arkansas has shown that of the total dry weight in a first position boll, the subtending leaf provides about 50%, the nearest main-stem leaf 35% and the remainder comes from leaves elsewhere on the plant, including leaves futher out on the fruiting branch. By the time a boll reaches its peak carbohydrate demand, it is usually buried in the canopy and the leaves surrounding it are in dense shade. Thus, as the boll ages it must rely on leaves further away at the top of the plant.

Carbohydrate Sources to a 1st Position Fruit

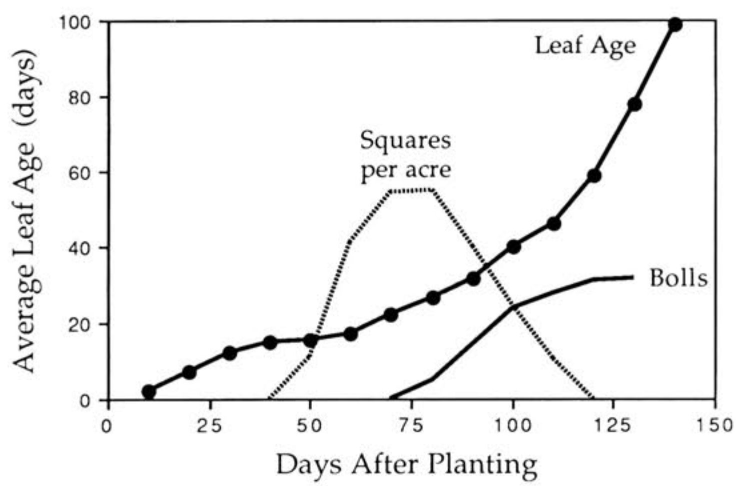
1st Position Fruit Stage	Major Food Sources	Function of Main-stem Leaf	Function of Subtending Leaf
Pinhead Square	Bracts	Unfurling	Microscopic
Large Square	Bracts + Main-stem Leaf	"Source"	Unfurling
Small Boll	Bracts + Main-stem + Subtending Leaves	"Source"	"Source"
Medium Boll	Bracts + Subtending Leaf	Declining	"Source"
Large Boll	Leaves at Top of Plant + Subtending Leaf	Declining	Declining

During the boll filling period, not only are the leaves rapidly aging but also the day length, air quality and temperature are deteriorating, further reducing the supply of carbohydrates to fill bolls. Management practices are aimed at bringing boll demand into better synchrony with leaf output. This is accomplished by both maintaining healthy leaves and promoting earliness of boll retention. The following table from studies by Wullschleger and Oosterhuis shows the percent of the total leaf surface that is exporting carbohydrates at different stages of crop development.

Leaf Age at Various Days after Planting

Leaf Age (days after unfolding)	Leaf Activity	Days After Planting: 60 1st Square	90 Bloom	120 Boll Fill
0-14	"Sink"	36%	11%	3%
15-28	Stong "Source"	38%	21%	11%
+29	Declining "Source"	26%	68%	87%

This same lack of synchrony with individual leaves and bolls is summed up by the timing of fruit development versus average leaf age. In the following diagram, average leaf age increases rapidly when the plant needs healthy young leaves to fill bolls.



The Plant Canopy is More Than its Leaves

Although we focus on individual leaves to learn how to maintain their nutrient output, it is the distribution and location of leaves in the plant canopy that determine whether bolls get filled. Just like any well designed organization, the cotton plant can do fine without any one specific leaf. The plant will accommodate by moving nutrients from other leaves. Two exceptions to this include the cotyledons during early seedling growth and the subtending leaf during early boll growth. The subtending leaf provides most of the nutrients to the young boll and if this leaf is shaded or damaged, that young boll will shed.

The total sum of leaves, or plant canopy, on the other hand, is highly significant. To sustain boll production cotton needs a plant canopy where young healthy leaves are illuminated. For this reason it is important to keep in mind the effect of management on the plant canopy and not just individual leaves. For example, if a post-directed herbicide injures lower canopy leaves, this would be much less detrimental than the same amount of injury caused by an "over the top" herbicide that affected young active leaves and stunted development of new leaves.

Water Stress Injures Leaves

Since cotton's peak leaf output and boll demand occur at different times, for maximum yield it is imperative that we avoid further separation of boll demand from leaf output. Avoiding a delay in boll setting is one critical management practice (discussed in next month's newsletter "Earliness and Shortseason". Likewise, avoiding practices that decrease leaf function will contribute to maximum yield. Water stress during boll filling is a Beltwide problem that decreases leaf function in multiple ways.

- Water stress shortens the useful life of a leaf and lowers its maximum output or "source" strength.
- Water stress causes the plant to cease developing new leaves, making the developing boll load totally dependent on the aging leaves.
- And finally, water stress restricts leaf size. In arid climates, where humidity is low, even well-watered fields will produce leaves with only half the surface compared to the humid Mid-South. In fact, excess leaf size is a problem in the Mid-South that requires close attention to fertilization. (see below)

Clouds Decrease Photosynthesis

On overcast days when light levels seem adequate for humans, plants actually are starving for light. Low cumulus clouds especially restrict light more than high cirrus clouds. Clouds can be especially detrimental during warm weather because the plant respires more, burning more energy just to stay alive. Because of the importance of cloud cover the GOSSYM cotton model incorporates light intensity into its photosynthetic calculation. Dave Albers of the GOSSYM COMAX Information Unit has calculated that cloudy overcast days, even without rain, can cut cotton's dry weight gain by 40%. When cloudy weather sets in during bloom, shed of small bolls is right around the corner.

Nutrient Deficiency Decreases Photosynthesis

Nutrient levels, especially N and K, can influence leaf size and photosynthesis. Nitrogen availability controls leaf size and the plants ability to produce new leaves. High N levels result in large leaves, especially if the humidity is high and the plant well-watered. Scientists in Arkansas recommend keeping N availa-bility at a moderate level pre-bloom, and then fertilizing for boll filling. This practice avoids large leaves that shade young bolls resulting in shed. While in the arid climates, where premature cutout is the problem (not large leaves), producers often apply the bulk of their N either pre-plant or soon after planting.

The deleterious effect of N deficiency on "source" strength under commercial practices, is on leaf size and new leaf production, and apparently not on the photosynthetic mechanism. On the other hand, potassium deficiency does decrease photosynthetic ability. When K levels in the petiole drop below 1.5%, that leaf is no longer a "source" of carbohydrates. This occurs when a heavy boll load exceeds the soil's ability to supply K and causes premature fiber termination and thus reduced micronaire in late set bolls.

Smog Decreases Photosynthesis

Cotton is one of the most sensitive crops to ozone damage due partially to its open stomates when ozone levels peak during the afternoon. Current lint yield loss in high ozone areas, such as the San Joaquin Valley, ranges from 10 to 20 percent. Ozone damages cotton leaves by eating away at the photosynthetic machinery disrupting its function and consuming energy in its repair. Ozone damaged leaves also age prematurely, turning yellow and flecked, due to their stressful environment.

Managing Sources/Sinks in Short-Seasons

A critical management concept for both long and short-season cotton producers is the need to balance "sinks" with "sources" during boll filling. The optimum balance of "sinks" to "sources" will derive from adjusting leaf area to yield potential. Let's look at this concept for a short production season, such as the Texas High Plains, where yields range from less than half a bale to over 2 bales per acre. When planting is delayed, Texas producers need to produce a canopy that can support and mature a 1 to 1.5 bale yield. They don't need a 4 to 5 foot plant. Management is focused on rapid leaf and fruit growth. Loss of early leaf area is almost as detrimental as loss of early fruit, and cutout rarely occurs before the temperature runs out. Under these conditions, plant height in excess of 36 inches is seldom beneficial. Management of late planted fields in warmer regions is also focused on early boll set and containment of plant height, however rapid canopy development is seldom a problem in these fields.

Managing Source/Sinks in Long-Season Regions.

Fields that are planted early and get off to a vigorous start in warm growing regions also need to balance "sinks" with "sources", but the optimum balance occurs at a greater leaf area and with taller plants. For these production regions, managing cutout is critical to top yield, because cotton will cutout or cease vegetative growth when the "sinks" consume all of the nutrients produced by the "sources". If "sinks" are few and/or "sources" strong, cutout is delayed. This happens when few bolls are set on the plant or when producers maintain strong "sources" by minimizing nutrient and water stress during boll filling. On the other hand, if many bolls are set and/or leaves are damaged, the plant will cutout prematurely without producing a top crop or adequately filling late set bolls. In these long growing regions, producers assess the boll load or "sinks" and compare it to the "source" strength. If the boll load is strong compared to the "sources" they maintain healthy leaves by insuring ample nitrogen and water. On the other hand, if boll load is slight, they avoid pushing "source" strength further and instead restrain leaf expansion while increasing fruit set with plant growth regulators.

Plant map data from 65 locations in the San Joaquin Valley was sorted to look at boll retention and plant height in the highest, lowest and average yielding fields. The highest yielding fields set a normal crop in the lower and middle zones, but sustained retention for 3 extra nodes in the top of the plant. Although boll size was not measured in these trials, from other work we can surmise that since retention was sustained longer, boll size was also sustained and the normal decrease in boll size with plant age was delayed. A strong clue to the management of these top yielding fields lies in their plant height. They were 8 inches taller than the average yielders due to ample fertility and irrigation, which kept top leaves from aging prematurely.

WRAP-UP

It is unfortunate that cotton has its greatest need for a vigorous canopy to fill and mature bolls when the plant and environment is deteriorating due to leaf aging, day length, air quality, nutrient availability and often low temperature. Regardless of the length of the growing season, maximum yield is associated with management practices that provide young healthy leaves during this critical boll filling period. These include sufficient mid-season nutrition, and avoidance of water stress, insect and chemical damage to critical upper canopy leaves. As we continue to improve varieties and production technology, maintenance of healthy young leaves during bloom and boll filling will become even more critical to the yield increases that these advancements provide.

Herbicide Injury to Leaves

Dave Guthrie and Alan York

Post-emergence herbicides provide extended protection to cotton and supplement soil-applied treatments. Compared to corn or soybeans, relatively few post-emergence herbicides are available to control broadleaf weeds and nutsedges in cotton. Additionally, young cotton is less competitive than other crops. To compensate for this limited arsenal of cotton herbicides and cotton's poor early season competitive growth, precise and timely procedures must be followed to afford maximum weed control and minimum crop injury. Herbicide injury to cotton leaves can have season-long effects resulting in delayed maturity, reduced yield and quality.

Herbicide injury in sensitive species is related to the physiological mode of action of the specific materials. Some herbicides, such as the triazines and ureas, interfere with the process of photosynthesis while others, such as the arsenicals, prevent efficient respiration. Phenoxy herbicides, such as 2,4D, disrupt the normal coordination of cellular growth and result in the characteristic malformed and twisted tissue. Additional indirect effects, including membrane leakage, also contribute to the loss of cellular integrity that leads to plant tissue death.

These physiological disruptions can be observed in cotton when insufficient herbicide application precautions have been taken. Delayed development is commonly observed following initial herbicide injury. This delay may result from several causes and may lead to delayed maturity. In our work with fluometuron (cotoran), "over the top" sprays delayed the onset and prolonged the boll-loading period. Plant mapping data indicated that the development of fruiting branches had been delayed. The leaf injury from this "over the top" application reduced the active leaf area restricting the total plant energy supplies available for plant growth. Alternately, research on MSMA suggested that another mechanism was delaying maturity, reduced boll set at the lower main stem nodes.

The delayed maturity can have further consequences. In addition to exposing the crop to increased insect pressure, thereby increasing production costs, delays in maturity can reduce yield and quality. Yield can be dramatically reduced in the northern regions of the cotton belt by autumn frosts. Herbicide-induced maturity delays heighten this danger. Additionally, boll development under cooler temperatures affects lint maturity and quality.

The most difficult weed management challenge confronting cotton producers is the avoidance of cotton injury during early post-directed herbicide treatments. Some leaf injury is unavoidable. Fortunately, crop recovery is usually rapid if the cotton terminal is unaffected. The lowest leaves on the plant are not crucial to early boll set. Herbicide contact on leaves destined to feed bolls, those leaves in the middle and top of the canopy, is more troublesome and should be avoided.

If cotton sustains herbicide injury, production practices should be modified to alleviate the resulting developmental delays. Plant height may rebound following herbicide injury. This may result from decreased boll load or "sink" strength. If herbicide applications delay boll set, it is important to avoid further boll shed due to shading. Insect management should be heightened. Fertilizer nitrogen may need to be reduced to avoid rank growth which further delays maturity.

Herbicide injury to cotton does not necessarily mean reduced yield. Results from published reports indicate acceptable, albeit delayed, yield development following herbicide injury if growing conditions are favorable and management strategies are adjusted.

About the Authors

Derrick Oosterhuis and Tom Kerby have been regular contributors to "Cotton Physiology Today". Derrick and Tom are cotton physiologists associated with The University of Arkansas, Department of Agronomy and University of California, Cooperative Extension, respectively. Dave Guthrie is the Cotton Extension Specialist for North Carolina and currently leading the resurgence of cotton to his state now that the boll weevil has been eradicated. Alan York is on the faculty at North Carolina State University. Alan has worked in cotton as both the former Extension Cotton Specialist and currently weed control researcher.

Cotton Physiology Field Seminars Planned

In cooperation with various Extension Specialists we are planning field seminars to train producers in cotton plant mapping and cover specific cotton physiology topics of local concern. These field days are open to the public, but are designed specially to address producer and consultant questions about plant mapping, and how to use a knowledge about cotton development in their management practices. For detailed information about each seminar, please contact us at the National Cotton Council or your local Extension Agent.

Louisiana, June 18, 9:30 to noon, at the N.E. Research Station, located 1 mile south of Winnsboro. Topics: Plant Mapping to Identify Field Problems, Physiology and Entomology of Current Crop Status, Speakers: Tom Burch, Jack Baldwin and Kater Hake.

Texas, June 19, afternoon, at the Stiles Farm Field Day, on Hwy 79 in Thrall Texas.

Tennesse, June 21, Please contact your local County Agent for details.

South Carolina, June 25-26, Please contact your local County Agent for details.

Cotton Physiology Binders Available

Several of you have asked that we develop a Physiology Binder to store newsletters and special projects being developed by Cotton Physiology Education Program . We now have 3 ring binders available at no cost. If you would like a binder with a copy of the publications, "Beginning Plant Mapping" and "Cotton Growth and Development for Production Agruiculture", please write to us at the National Cotton Council in Memphis.