Chapter 4

LIGHT AND THE COTTON PLANT

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INTRODUCTION

Light is the energy that supports all life on earth. It is also the energy that photosynthesis of ancient plants for creating the carbon that was the basis of fossil fuels. Today the sun's energy also powers photosynthesis and is involved in a myriad of plant processes that influence how plants develop and grow. This review will explore these processes.

WHAT IS LIGHT?

To humans, light is that portion of the electromagnetic radiation spectrum (ERS) that our eyes can detect. It is in fact only a small portion of the ERS (Fig. 1) that includes radiation wavelengths ranging from gamma rays to TV and radio. This small sliver of the ERS closely corresponds to the wavelengths that are utilized to drive plant photosynthesis, namely 400 to 700 nm or photosynthetically active radiation (PAR). However, this small range is not the only part of the radiation spectrum that affects plant growth and development. The presence of neighboring plants will alter the light environment through reflection from, and transmission through, plant tissues. Reflected and transmitted light will be enriched in far-red light in relation to red light. Both far-red and red light can be detected through phytochrome, a photoreceptor pigment in plants that changes form in response to red or far-red light and their ratio (Fig. 2). There are also blue light receptors, phototropins and cryptochromes, which mediate responses to the blue wavelengths of light. Mediation of growth and development in response to light environment is called photomorphogenesis and may include germination, (de)etiolation, and shade avoidance. Much of the initial knowledge concerning photomorphogenesis was obtained from experiments that utilized the Beltsville Spectrograph developed by Drs. Harry Borthwick, Marion Parker, and Sterling Hendricks at the USDA research center at Beltsville, MD (Kasperbauer, 1992). They passed a light source through two prisms that separated the light beam into its constituent components, much like a rainbow (Fig. 3). They placed plants into these separate light zones and observed the effect on plant growth. Through this work and other experiments the theory of phytochrome was developed and subsequently led to its discovery.

LIGHT INTERACTION WITH COTTON LEAVES

Leaves of *Gossypium hirsutum* "track" the light throughout the day. In other words, the leaves remain perpendicular, or mostly so to the impinging sunlight (Fig. 4). Ehleringer and Hammond (1987) found that the cosine of incidence of impinging radiation on *G. hirsutum* leaves was nearly one for the core hours of 0700 to 1500 hours. This observation is significant

due to Lambert's Cosine Law which states that the intensity of radiation is a function of the cosine of the angle from the perpendicular. If the angle of light impingement is 0 (the angle light is striking the surface is perpendicular), the cosine is 1. The law is also known as the cosine emission law or Lambert's emission law. It is named after Johann Heinrich Lambert, from his Photometria (Lambert, 1760).
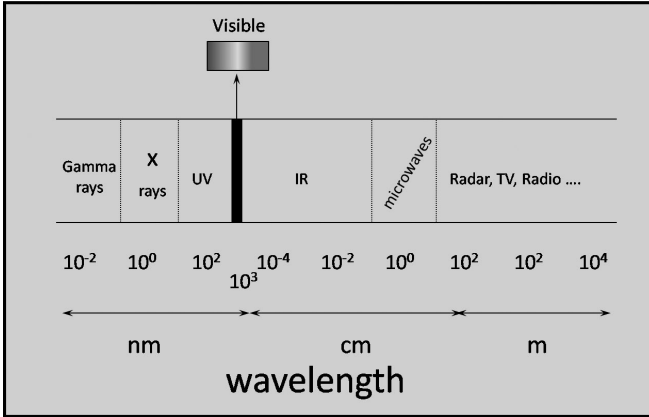
Figure 1. The electromagnetic radiation spectrum contains the relatively small range visible to the human eye, which closely corresponds to the wavelengths utilized in photosynthesis.
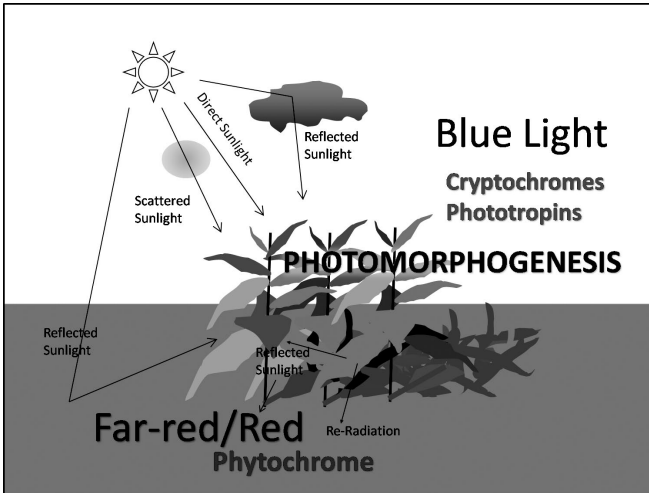
Figure 2. The various ways plants interact with light as affected by both the environment and neighboring vegetation and results in reflected, reradiated, scattered, and direct sunlight. Sensing mechanisms include both red/far-red (phytochrome) and blue (cryptochrome and phototropin) absorbing pigments.
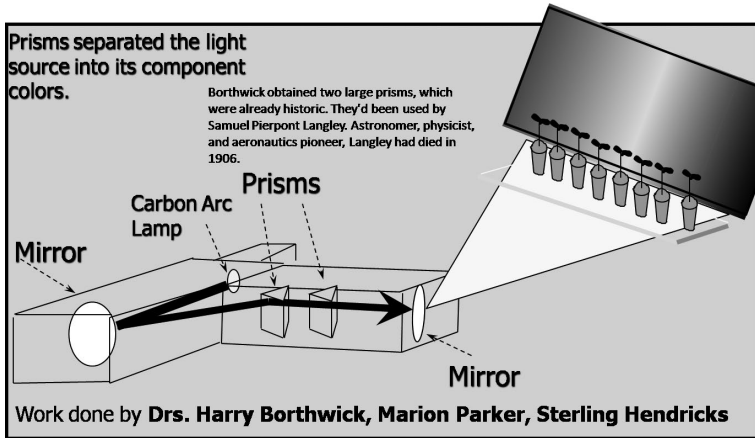
Figure 3. The Beltsville spectrograph used prisms to separate light into its component parts, thus allowing the study of finite wavelength ranges on plant growth and development.
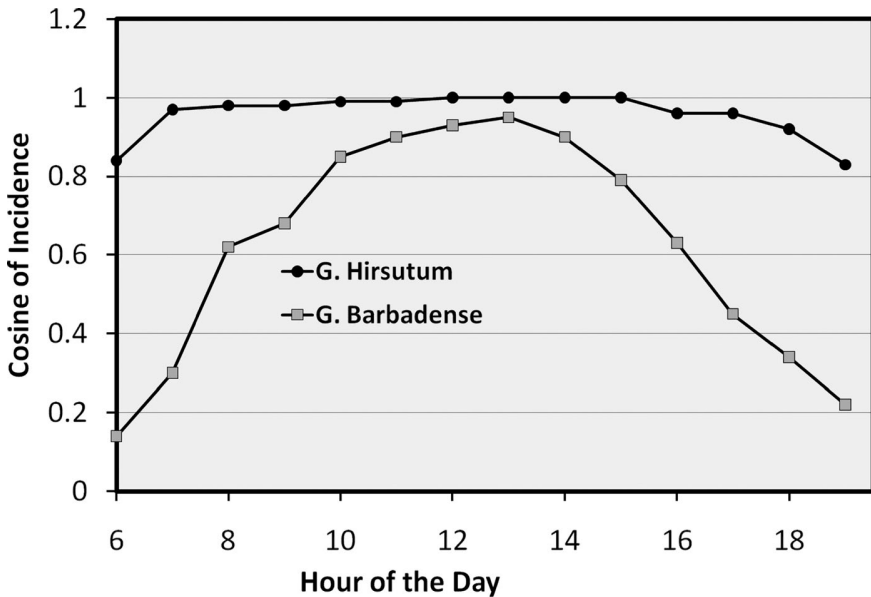

Figure 4. The diurnal course of the cosine of the angle of incidence for leaves of *Gossypium hirsutum* cv. Stoneville 825, and *G. barbadense* cv. Pima S5. Data are from Phoenix, AZ. (Adapted from Ehleringer and Hammond, 1987).

Such movement of upland cotton with the sun's position maximizes the available sunlight to power photosynthesis. Interestingly, *Gossypium barbadense* does not show a change in leaf position throughout the day. We know Lambert's Cosine Law through our own life experiences. The change of seasons is due to the changing angle of incidence that sunlight exhibits due to the earth's tilting and further explains the differing daylengths seen with changing latitude throughout the year.

The photosynthetic response of cotton leaves to PAR intensity may be seen in Figure 5. Although the okra-leaf cotton photosynthetic rates found by Pettigrew (2004) were greater than the normal-leaf, all showed little increase at a PPFD above 1,000 $\mu mol\ m^{-2}\ s^{-1}$. This threshold also exists for canopy photosynthesis rates which are maximized at a PPFD of 1,200 $\mu mol\ m^{-2}\ s^{-1}$ (Wells, unpublished). These photosynthetic responses to light are typical of C3 photosynthetic metabolism.
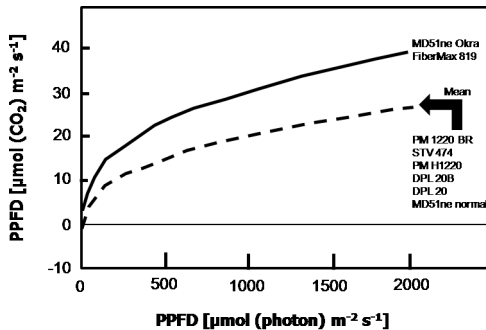
Figure 5. Mean photosynthetic response of two okra-leaf and six normal-leaf cotton genotypes to varying photosynthetic photon flux density (PPFD) in 1998 at Stoneville, MS. (Adapted from Pettigrew, 2004).

TOO LITTLE LIGHT

Goodman (1955) stated "this inability of some varieties (cotton) to respond to all cloud events may provide evidence in favour of the usually postulated mechanism of temporary carbohydrate shortage within the plant as being the fundamental cause of shedding during periods of cloudy weather". He was explaining the consequences of too little light during the season in Sudan. The work of Zhao and Oosterhuis (1998) using shading shelters in field-grown cotton during squaring, flowering and boll development, supported this. They showed that reduced light (63%) significantly decreased photosynthesis and carbohydrate concentrations in leaves and bolls, resulting in increased fruit abscission and decreased yield and fiber quality (Zhao and Oosterhuis, 1994). This phenomenon was also addressed in research of Pettigrew (1994) in which 30% shade was imposed on cotton during reproductive development (Table 1). The un-shaded control treatment exhibited lint yield, percentage yield at first harvest, and bolls per m^2 values that were 24, 10 and 26 % greater than the 30% shade treatment, respectively. In the same study, light was increased to lower canopy strata by either reflection or opening the canopy by restraint of neighboring rows. These treatments led to 6 and 17% greater fiber yield than observed in the untreated control, respectively. Both shade and enhancement of light penetration to lower canopy leaves demonstrate that photosynthate production is the ultimate determinant of cotton productivity.

Table 1. Lint yield, first harvest percentage boll mass, lint percentage, seed mass, and boll number averaged over 1991 and 1992.

Treatment	Lint Yield kg/ha	First Harvest %	Boll Mass g	% Lint %	Seed Mass mg	Boll Number no./m^2
Open canopy	1397	95.6	4.47	37.6	97	83
Reflectors	1261	93.6	4.44	37.7	98	76
Control	1190	92.7	4.41	37.8	99	72
Shaded Plot (30%)	957	84.0	4.44	37.7	98	57
LSD (0.05)	68	1.9	ns	ns	ns	4

(Adapted from Pettigrew, 1994).

PHYTOCHROME MEDIATED RESPONSES

A classic shade avoidance is seen in many plant species. This response entails photomorphogenesis including an increased nodal length, increased height, and a reduction in branching in response to shade which is enriched in far-red (FR) light. Ouedraogo and Hubac (1982) described such a response when the 9-hour light period was ended with 30 min. of FR light exposure. In a subsequent experiment, they found lower root mass and higher shoot dry weight/root dry weight ratio when the light period ended with 30 min. of FR light (Ouedraogo *et al*., 1986). The ending FR would convert the FR form of phytochrome (Pfr) to the R form of phytochrome (Pr) thus resulting in the morphological alterations observed. Smith *et al*. (1990) showed that the R/FR light ratio increased as a sensor was moved away from an artificial canopy of tobacco. In addition, the ratio of Pfr/Ptotal increased as a cuvette containing purified phytochrome was moved in a similar manner. These results showed that it was possible for plants to sense neighboring plants despite not being directly shaded by their presence, an important bit of knowledge when comprehending population effects on crop growth.

Light environment may also be altered by using different colored mulches. Kasperbauer (1994) used white, red, and green mulches in field-grown cotton (Table 2). He found the plant height, fiber yield and boll number were increased 10, 27, and 26% when red mulch was utilized instead of white. These same parameters were increased by 13, 23, and 21% when green mulch was used instead of white. In another study, fiber length was almost 4 mm longer in plants that were grown over the high FR/R reflectors (3.79 and 3.78 mm for green and red, respectively) than when grown over surfaces that reflected more photosynthetic light (1.07 and 0.94 mm for aluminum and white, respectively). This elongation response is very similar to stem elongation responses reported by Ouedraogo and Hubac (1982).

Table 2. Characteristics of mature cotton plants after growth from emergence through maturity over different colored soil covers (mulches) in trickle irrigated field plots near Florence, SC. Values are 2-year means ± SE. Seed cotton includes seed with fibers attached. Fiber and seed weights were determined after ginning.

Plant Characteristic	White	Red	Green
Height (cm)	79±1	87±2	89±2
Bolls (no)	19±1	24±1	23±1
Seed cotton (g)	78±4	98±6	95+5
Fiber (g)	30±2	38±2	37+2
Seed (g)	45±2	57±4	56±3
Seed weight (mg)	94±3	105±4	I07±4
Fiber seed^{-1} (mg)	62±3	70+4	70+3

(Adapted from Kasperbauer, 1994).

ULTRAVIOLET MEDIATED RESPONSES

Ultraviolet light is light that comprises the wavelengths of 10-400 nm. The range most often studied in relation to plant growth is ultraviolet B (UV-B) or medium wave. Zhao *et al*. (2004) examined the effects of both elevated CO_2 concentrations and UV-B levels on cotton growth and development (Fig. 6). The intensities of UV-B chosen were zero, that which would be experienced on a sunny day in Mississippi (8 kJ m^{-2} d^{-1}), and that which would be equivalent to a 30% increase associated with loss of stratospheric ozone (16 kJ m^{-2} d^{-1}). They found that only the greatest intensity of UV-B resulted in reduced photosynthesis, namely decreases of 56 and 45% at 360 and 720 μL L^{-1} CO_2, respectively when compared with the 0 and 8 kJ m^{-2} d^{-1} UV-B intensities. Gao *et al*. (2003) showed that cotton plant growth was negatively affected by radiation supplemented with UV-B at 4.8 and 9.5% above that found in ambient light (Table 3). The 4.8% enhanced level decreased plant height, leaf area per plant, net assimilation rate, relative growth rate, and biomass per plant by 5, 19, 37, 29,and 12%, respectively. These same variables were reduced by the 9.5% enhanced UV-B by 24, 29, 42, 45, 34%, respectively.
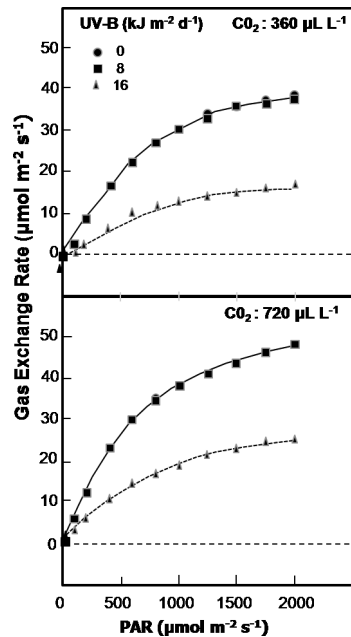
Figure 6. Photosynthetic light-response curves of cotton uppermost fully expanded mainstem leaves at first flower stage as affected by elevated [CO_2] and UV-B radiation. Data are means ± SE of three measurements. (Adapted from Zhao *et al*., 2004).

Table 3. The comparisons of cotton growth under different UV-B treatments.

| UV-B Treatment	Plant Height (cm)	Leaf Area (cm²/plant)	Net Assimilation Rate (g/m²/d)	Relative Growth Rate (g/g/d)	Biomass (g/plant)
Ambient	104	3709	8.3	0.068	168
+ 4.8%	99.5	3000	5.2	0.048	148
+ 9.5%	89.5	2626	4.4	0.044	110

(Adapted from Gao *et al*., 2003).

TOO MUCH LIGHT

While maximizing light exposure is desirable for maximum plant productivity, there are situations when too much light can cause physiological harm to cotton. Payton *et al*. (1997) found about a 60 % inhibition of photosynthesis in response to a 3 hour exposure to 1,300 μmol m^{-2} s^{-1} at 5-7°C in both a normal genotype and a genotype with overexpressed Mn superoxide dismutase activity (Fig. 7). These 'photoinhibitory' effects have been also observed at milder temperatures. Königer and Winter (1993) observed reductions in photosynthetic rate of about 30 to 40% at a temperature as high as 20°C when exposed to either 1,000 or 1,800 μmol m^{-2} s^{-1} (Fig. 8). Photoinhibition can be caused by visible light (V), by ultraviolet light (UV), and by the interaction (UV-V) (Powles, 1984). These wavelengths may be involved with another pigment often seen in cotton, anthocyanin. Anthocyanin is the red color that appears in cotton especially in later stages of growth. It has been implicated in the absorption of UV light. In a study we conducted (Wells, unpublished) in North Carolina, plastic frames were attached to main-stem leaves and they were inverted and held in place so the abaxial surface was exposed to sunlight (Fig. 9A). The result was an increase in anthocyanin concentration in leaf tissue that were not covered by the frames (Fig. 9B). The anthocyanin concentration in the inverted leaves exhibited 20 to 50% increases over that in the non-inverted leaves. It has been suggested that anthocyanin plays the role of a sunscreen Gould (2004) reported that anthocyanins offer protection by two processes, by acting as a mask for filtering green light and by scavenging reactive oxygen species, thereby reducing the losses from photoinhibition after leaves are exposed to strong light. Purified anthocyanin scavenges almost all species of reactive oxygen and nitrogen with an efficiency up to four times greater than those of ascorbate and α-tocopherol. He also proposed that higher incidence of anthocyanins in stress environment is the last line of defense against ROS and photoinhibition after all other mechanisms of protections have been exhausted. Hoch *et al*. (2003) theorized that anthocyanins protect foliar nutrient resorption during senescence in certain tree species by protecting photosynthetic tissues from excess light. Using wild type and anthocyanin-deficient mutants of three deciduous woody species, they found wild type plants maintained higher photochemical efficiencies than mutants and were able to recover more easily from the effects of a high light, low temperature environment than could the mutants. Based on these reports it is possible that the anthocyanin increase in the inverted leaves is induced as a photo-protectant from light directed at tissue that is normally unexposed.
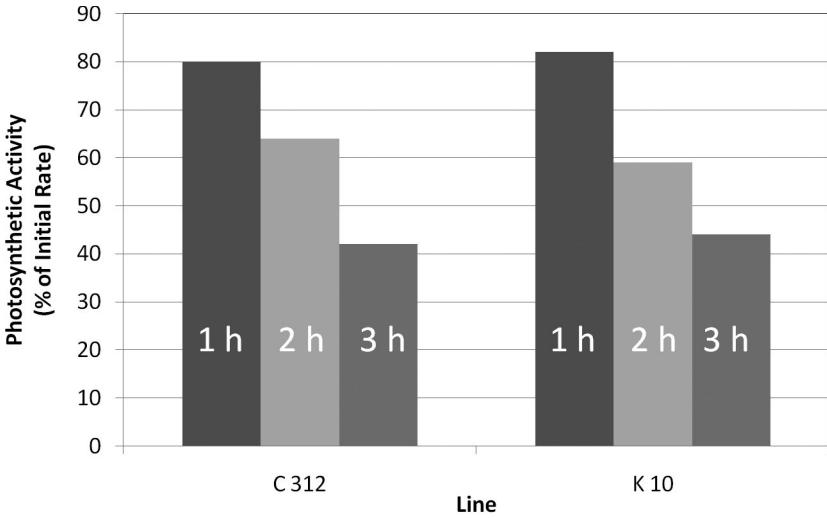
Figure 7. Steady-state photosynthetic activity at 25°C as a percentage of the activity prior to an exposure to a PPFD of 1300 μmol m^{-2} s^{-1} at 5-7°C for 1 h, 2 h, and 3 h for leaf discs from plants of Coker 312 and Mn superoxide dismutase transgenic line, K10. (Adapted from Payton *et al.*, 1997).
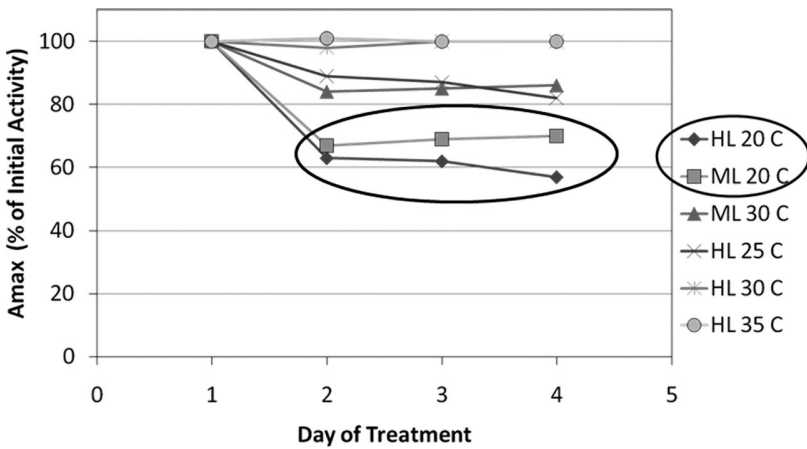
Figure 8. Changes in gas exchange parameters of sun leaves of *Gossypium hirsutum* during 4-d treatments. Leaves were exposed to either 1,800 μmol m^{-2} s^{-1} (HL) or 1,000 μmol m^{-2} s^{-1} (ML) at air temperatures of 35, 30, 25, and 20°C, respectively. Maximum CO$_2$ assimilation rates (A$_{max}$) of each quantum level are expressed as percent of the initial values measured at the onset of treatments. (Adapted from Königer and Winter, 1993).
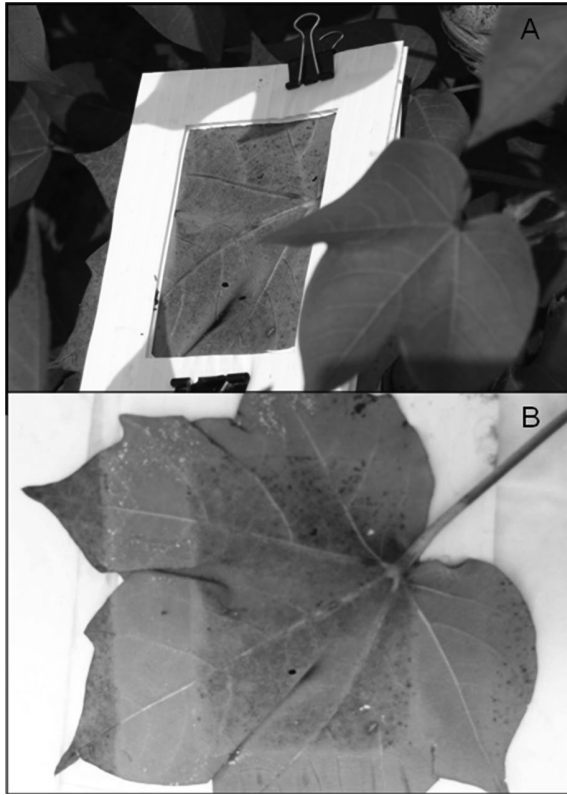
Figure 9. A. The plastic frame used to hold the leaf in a position that presents the adaxial to sunlight, and B. the leaf with the frame removed. Note the lack of red color where the frame was situated.

SUMMARY

Man's eye can detect only a small portion of the electromagnetic radiation spectrum (ERS) and this range closely corresponds to the wavelengths that are utilized to drive plant photosynthesis, namely 400 to 700 nm or PAR. There other wavelengths of light that fall outside of the PAR range that are involved in altering growth and development in response to the environment. Light will be reflected by and will be transmitted through neighboring plants and will alter the light environment. Reflected and transmitted light will be enriched in far-red light in relation to red light. Both far-red and red light can be detected through phytochrome, a photoreceptor pigment in plants that changes form in response to red or far-red light and their ratio. Phytochrome plus the blue light receptors, cryptochromes and phototropins, cause alterations in plant growth and development called photomorphogenesis. In addition, UV light can negatively affect cotton photosynthesis and growth when present at a sufficient intensity. Both too little light and too much light can have negative effects on cotton growth through effects on photosynthesis. Too little light fails to produce photosynthate in sufficient quantity to maximize growth thus leading to fruiting form shedding. Too much light, especially in the presence of low temperatures, causes reduced photosynthesis through photoinhibition. In either case, crop productivity is reduced. One thing is for sure, changing light environments will bring about change either through direct effects on photosynthetic capacity or through photomorphogenesis.

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