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Cotton plant size and fiber developmental responses to FR/R ratio reflected from the soil surface

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Cotton (*Gossypium hirsutum* L.) plants were grown in irrigated field plots over red, green or white soil covers (mulches). The far-red (FR) to red (R) light ratios were higher in upwardly reflected light over the red and green surfaces than in incoming sunlight. Plants that grew over the white mulches received higher photosynthetic photon flux (PPF), but the reflected FR/R ratio did not differ significantly from that in incoming sunlight. At five weeks after emergence, seedling stem lengths were significantly longer over red and green than over white surfaces. At maturity, plants that had grown over the red and green surfaces had longer stems, larger shoots, more bolls (fruit), more seed cotton, and longer fibers than plants grown over the white surfaces even though those grown over the white surfaces had received more reflected photosynthetic light during growth and development.

Key words – Cotton, far-red/red ratio, *Gossypium hirsutum*, phytochrome, reflected light.

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Introduction

Photosynthesis and the partitioning of photoassimilates are both important in cotton (*Gossypium hirsutum* L.) plant growth and in the development of seed and fiber. Canopy architecture and the interception of photosynthetically active light (400–700 nm) have received considerable attention. However, the spectral distribution of light acts through morphogenic pigments, such as phytochrome, within the plant to regulate how the photoassimilate is distributed and used.

Phytochrome regulation of plant physiological processes has been studied extensively under controlled environments. Borthwick et al. (1952) discovered red (R)/far-red (FR) photoreversible control of seed germination. Downs et al. (1957) found R-FR photoreversible control of stem elongation in seedlings. Detailed action spectra for regulation of morphological responses were conducted on the Beltsville Spectrograph by Borthwick, Hendricks and their colleagues to study the efficiency of photons at different wavelengths for regulation of plant responses such as seed germination and floral induction (Borthwick 1972). Many of the studies involved short irradiation periods in search of an "on-off" control mechanism. Phytochrome action peaks for seed germination and absorption peaks in vitro were determined to be near 660 nm and 735 nm for the red-absorbing (P_r) and the far-red-absorbing (P_{fr}) forms, respectively (Borthwick et al. 1952, Butler et al. 1964). In green plants, however, the action peak was at about 645 nm for P_r because of competitive absorption at 660 nm by chlorophyll, and morphological responses to irradiation at 735 nm differed significantly with short or prolonged treatment durations (Kasperbauer et al. 1963). This background has been highly relevant in interpretation of recent studies of phytochrome regulation of field plant growth and development.

Early attempts to relate phytochrome action to field plant development included measurement of spectral shifts in tobacco (*Nicotiana tabacum* L.) canopies (Kasperbauer 1971). This approach revealed decreased photosynthetic photon flux (PPF) and decreased blue as well as shifted FR/R ratios within the plant canopy. A controlled environment experiment with hydroponic-grown tobacco seedlings showed R-FR photoreversible control of shoot/root biomass ratio. Plants that received FR treatment (a

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high FR/R ratio) in the controlled environment were morphologically and chemically similar to close-spaced plants in the field. It was proposed that the amount of FR and the FR/R ratio were the dominant factors in morphogenic adaptation to population density under field conditions.

In the early 1980's, an improved spectroradiometer was used to document that FR reflected from green leaves of competing plants is a major contributor to the FR/R ratio received by growing plants under field conditions (Kasperbauer et al. 1984). Morphogenic responses to FR reflected from competing plants have been demonstrated for a number of plant species (Kasperbauer and Karlen 1986, Ballaré et al. 1987, 1990, Kasperbauer 1987, 1992, Kaul 1988, Casal and Smith 1989, Smith et al. 1990, Mancinelli et al. 1992). Each green leaf absorbs most of the visible light and reflects or transmits much of the FR. The FR reflection curve begins to plateau at about 750 nm, well beyond the absorption peak for P_{fr}. Thus, the FR/R ratio received by a growing plant in the field is influenced by the number, size, nearness and even heliotropic orientation of competing leaves. Plants in higher-density populations receive more reflected FR and higher FR/R ratios, and they adapt to competition from other plants by developing longer stems at the expense of new root growth (higher shoot/root ratios). In nature the ecological significance of this phytochrome-regulated photoassimilate allocation response to reflected FR favors survival by increasing the probability that the longer stems will allow some leaves to be in sunlight above the competing plants.

After realizing that FR reflected from competing plants in various field population densities influenced the FR/R ratio and phytochrome regulation of photosynthate partitioning among plant components, it was hypothesized that the FR/R ratio reflected from different colors of soil or from artificially colored soil surface covers (mulches) might also affect plant development via the phytochrome system. The approach allows plants to grow in summer sunlight for photosynthesis, but they receive a modified FR/R ratio in upwardly reflected light to regulate partitioning of photoassimilate within the growing plants. It was further hypothesized that a FR/R ratio higher than the ratio in incoming sunlight (as occurs among close-spaced plants) should favor shoot growth, whereas a FR/R ratio lower than the ratio in sunlight should favor root growth. In the first field test of this concept (1986), tomato (*Lycopersicon esculentum* Mill.) plants grown over a surface that reflected a FR/R ratio about 10 to 15% higher than that in incoming sunlight produced more and larger tomato fruits than plants grown over the commonly used black or white mulch surfaces, which reflected FR/R ratios similar to the ratio in incoming sunlight (Decoteau et al. 1989).

Cotton seedlings were also morphologically responsive to FR/R ratio in reflected light over different colored soils and mulches (Bradburne et al. 1989, Kasperbauer and Hunt 1992). Seedlings grown in summer sunlight over surfaces that reflected FR/R ratios higher than the ratio in incoming sunlight developed longer stems, larger shoots, less massive roots, and greater shoot/root biomass ratios. The objective of the present study was to compare the relationship of soil surface (mulch) color and characteristics of reflected light during growth to morphological characteristics of field-grown cotton plants at maturity.

Abbreviations – FR, far-red light; P_{fr}, far-red absorbing form of phytochrome; P_r, red absorbing form of phytochrome; PPF, photosynthetic photon flux; R, red light.

Materials and methods

Plant material and growth conditions

Cotton (*Gossypium hirsutum* L. cv. PD-1) plants were grown in irrigated field plots of Norfolk loamy sand (Typic Paleudults) at the Coastal Plains Soil, Water and Plant Research Center near Florence, South Carolina in 1987 and 1988. Each year, plots were fertilized according to recommendations of the Clemson University Cooperative Extension Service and ridge rows were prepared at 1-m intervals. Trickle irrigation tubes were placed on top of the ridges and the plots were covered with 6 × 20-m sheets of black plastic. The 6-m width covered four of the ridged rows, and there was an uncovered row between adjacent plastic-covered plots. There were three such plots each year. Each plot contained three 5.5 m long subplots which were painted with red, green or white exterior enamel to provide the desired reflection spectra. The sequence of colors was randomized within each plot. Exterior enamels were used because they provided an economical and repeatable method to obtain the desired reflection spectra for small plot studies.

Each subplot (color) consisted of four parallel rows (1 m apart), and 5-cm diameter holes were cut in the plastic at the top of the ridge to provide within-row plant spacing of 0.3 m. These spatial arrangements assured that plants would be exposed to light reflected from the mulches during the entire growth and development periods. Four seeds were sown in each hole on 21 May 1987 and on 9 May 1988. When the seedlings were in the cotyledon stage, all but one per hole were removed by cutting below the cotyledons. In this manner, roots of the remaining plants were not damaged, and the seedlings were exposed to the various patterns of reflected light from the time of emergence.

Upwardly reflected light

The quantity and spectral distribution of upwardly reflected light were measured 25 cm above the colored mulch surfaces using a LiCor (Lincoln, NE, USA) LI-1800 portable spectroradiometer equipped with a remote hemispherical light collector on a 1.5-m fiber optic probe. Measurements were made at 5-nm intervals between 400 and 800 nm. A reference spectrum was obtained by measuring incoming sunlight at the same wave-

Tab. 1. Characteristics of upwardly reflected light above the different colored soil covers (mulches). Values are expressed as percentages of incoming sunlight at the measured wavelengths, and as photon ratios in reflected light relative to the ratio in incoming sunlight (which was assigned a value of 1.00). Photon ratios were calculated before rounding off the mean values for R, FR and FR'.

Light characteristics	Mulch surface color		
	White	Red	Green
Percentage reflected			
PPF (400–700 nm)	43	15	12
R (645±5 nm)	43	34	9
FR (735±5 nm)	44	39	13
FR' (755±5 nm)	43	40	22
FR/R photon ratio in upwardly reflected light			
FR/R	1.01	1.14	1.44
FR'/R	1.00	1.17	2.41

lengths. Light measurements were taken on a cloudless day at solar noon ± 30 min. The reflected light values were then calculated as percentages of incoming sunlight at each measured wavelength. The FR/R ratios in upwardly reflected light were expressed relative to the FR/R ratio in incoming sunlight. The rationale for this approach was that field plants normally grow in sunlight with constantly changing characteristics and plants might be able to sense and respond morphologically to a light environment that differs in spectral distribution from incoming sunlight. The working hypothesis was that a FR/R ratio higher than the ratio in incoming sunlight should signal a different pattern of photoassimilate allocation and morphological development than would be obtained with the same FR/R ratio as is in incoming sunlight.

Plant measurements and sampling

Stem lengths were measured each year on 10 plants from each of the three replicate plots per color about five weeks after emergence. At maturity, each plant within the two middle rows of each 4-row subplot (color treatment) was measured for height, and the number of bolls (fruit) were recorded. When the cotton was ripe, seed cotton (seed with fibers still attached) was picked and weighed on an individual plant basis. Rows 1 and 4 of each subplot served as borders. The values for each color are means for 14 plants from each of the 2 sampled rows from each of 3 replicate main plots from each of 2 years, (i.e. 168 plants). The harvested seed cotton was ginned to separate fibers from seed. Fiber and seed were weighed on an individual plant basis, and 100 seeds were randomly selected from each of 2 randomly selected plants from each of the 6 sampled rows per color. The 100-seed lots were weighed to determine color treatment effects on seed size and the average amount of fiber per seed.

Fiber measurements

Fiber length and strength were measured on four fiber samples from each of the two sampled rows within each of the three replicate plots per mulch color from the 1988 experiment. The fiber measurements were conducted at the same commercial laboratory (Starlab, Knoxville, TN, USA) as is used by US Department of Agriculture Cotton Breeding Programs. Fiber properties were determined as follows: (1) 50% span length (50SL) = length at which 50% of the fibers are this length or longer; (2) 2.5% span length (2.5SL) = length at which 2.5% of the fibers are this length or longer; and (3) fiber strength as the force necessary to break the fiber bundle with the jaws of the testing instrument set 3.2 mm apart.

Results and discussion

Reflected light

The photosynthetic photon flux (PPF) and FR/R ratios in upwardly reflected light above the different colors are shown in Tab. 1. The PPF values in reflected light were higher over the white than over the red and green surfaces. These values were measured because many researchers of crop plant canopies have attempted to increase quantity of intercepted light as a means of increasing photosynthesis and plant yields. Values for R are shown for 645 nm rather than at 660 nm (the absorption

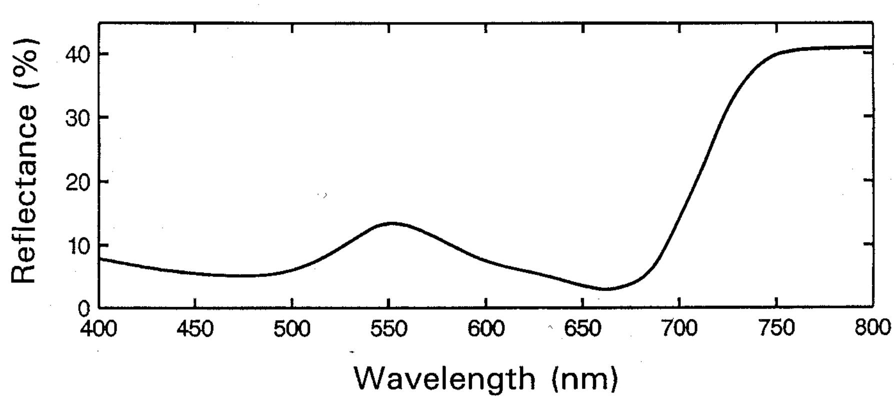

Fig. 1. Percentage of light reflected from the surface of a typical green leaf. The curve shows percentages of light reflected at each measured wavelength (at 5-nm intervals from 400 to 800 nm) relative to the quantity of incoming light at the same wavelengths. Measurements were made with a LiCor-1800–12 Integrating Sphere.

Tab. 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 characteristics	Mulch surface color		
	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	107±4
Fiber seed^{-1} (mg)	62±3	70±4	70±3

peak for P_r) because competitive absorption by chlorophyll at 660 nm shifts the P_r action peak in green plants to about 645 nm. Values for FR are shown for both 735 nm (the approximate absorption peak for P_{fr}) and at 755 nm which is just beyond the point at which reflection from a green leaf begins to plateau (see Fig.1). Also, highly refined action spectra developed on the Beltsville Spectrograph showed that when green plants were irradiated for a prolonged period, more distinct FR responses were obtained in the wavelength range of 750 nm to 770 nm than at 735 nm (Kasperbauer et al. 1963, Kasperbauer 1992). The green plant morphological response differences between short and prolonged irradiation at 735 nm were attributed to overlapping absorbancies of P_r and P_{fr} at 735 nm and the effect on photoequilibrium between P_r and P_{fr}. However, more recent studies (Smith and Whitlam 1990, Robson et al. 1993) suggest that intermediates or different phytochromes may be involved in regulation of morphological responses in the field. Another observation that is relevant toward interpretation of green plant morphological responses to FR was reported by Vogelmann and Björn (1984). They inserted fiber optic probes into fleshy green leaves and found that the measured amount of FR at about 750 nm was higher within the green leaf than at its exterior surface due to photon scattering, internal reflection and little competitive absorption at 750 nm within the tissue. The geometry of the plant part can also influence light scatter and reflection within the tissue (Seyfried and Fukshansky 1983). Thus, because of competitive absorption by chlorophyll at 660 nm and the possible enhancement of FR, the effective FR/R ratio within green tissue can be much higher than the ratio at the exterior surface. These factors all appear relevant in the interpretation of photomorphogenesis in field-grown plants. An important point in this discussion is that the amount of reflected FR at about 755 nm should be considered when attempting to explain wavelength balance and its involvement in regulation of photosynthate allocation in sun-grown plants under field conditions.

Seedling growth

Stem lengths averaged 49 and 47 cm, respectively, for 5-week-old seedlings grown in sunlight over green and red surfaces and only 37 cm when grown over white. It is of interest that stem elongation was greatest over the surface that reflected the highest FR/R ratio and lowest over the white surface, which reflected more photosynthetic light but the same FR/R ratio as was present in incoming sunlight. Since fiber is the economically important part of the cotton plant, it was important to evaluate characteristics of mature plants after they completed growth and development in field plots over the different colored mulches.

Plant characteristics at maturity

Plant size, the number of bolls (fruit), and the quantity of fiber at maturity are shown in Tab. 2. Although plants grown over red and green surfaces received less reflected PPF than plants grown over white, they received full incoming sunlight and higher reflected FR/R ratios; and they grew taller, developed more bolls per plant, and produced more fiber. Clearly, the increased amount of photosynthetic light beyond the amount in incoming summer sunlight did not result in greater shoot size, boll number or fiber productivity. However, the response pattern to FR/R ratio was consistent with the early seedling growth (see above and Bradburne et al. 1989). Development of a greater number of bolls over the red than over the white mulch surfaces was consistent with the results of a previous experiment with tomato in which plants that were grown over red surfaces produced more fruit than plants that had grown over white surfaces (Decoteau et al. 1989). In addition to the increased number of bolls per plant, those grown over the red and green surfaces developed greater fiber weight per boll (Tab. 2). This could possibly be attributed to heavier fibers of the same length, or to longer fibers. Samples of ginned fiber from plants grown over the three colors were measured to assess these possibilities.

Fiber characteristics

Fibers from plants that were grown over the red and green surfaces were longer than those from plants grown over

Tab. 3. Length of ginned cotton fibers after growth from emergence through maturity over different colored soil covers (mulches) in trickle irrigated field plots near Florence, SC. Values are means ± SE for 24 measurements (i.e., 2 measurements for fiber samples from each of 4 randomly selected plants from each of 3 replicates for each color).

Fiber characteristics	Mulch surface color		
	White	Red	Green
2.5SL (mm)	28.6±0.3	29.6±0.2	29.7±0.1
50SL (mm)	14.2±0.2	14.5±0.1	14.7±0.1

the white surfaces (Tab. 3). It should be noted that the longest fibers developed on plants that received the higher reflected FR/R ratios (Tab. 1) and also developed longer stems (Tab. 2). Values for fiber strength were numerically higher for fiber that developed in bolls on plants that were grown over the white surfaces than for those grown over the red and green surfaces. However, the differences were not statistically significant. Another interesting observation was that fibers from plants that received the greater amount of photosynthetic light (those grown over the white surfaces) were shorter (Tab. 3) and weighed less (Tab. 2).

In summary, it has been known for many years that an increased FR/R ratio can result in longer hypocotyls and stem internodes (Downs et al. 1957), longer petioles and increased leaf length to width ratios (Kasperbauer and Hiatt 1966, Sánchez 1971). The longer fibers on cotton plants that received higher FR/R ratios during development are consistent with the other morphological responses described above. Nevertheless, it is the first documented evidence of FR/R effects on cotton fiber length. The morphological effects of light ratios reflected from the soil surface raises an interesting question of whether geographic differences associated with plant product quality might be influenced by natural soil color or by the color of plant residues left on the soil surface in minimal tillage crop production systems. It also introduces a potential method to modify cotton fiber length by changing mulch surface color where mulches are already used to control water loss by blocking evaporation from the soil surface, and to control weeds without applying chemical herbicides to the soil as an approach to more environmentally friendly agriculture. More detailed studies on effects of light spectra during cotton fiber development are in progress.

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