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COTTON SEEDLING MORPHOGENIC RESPONSES TO FR/R RATIO REFLECTED FROM DIFFERENT COLORED SOILS AND SOIL COVERS

MICHAEL J. KASPERBAUER* and PATRICK G. HUNT
USDA, ARS, Coastal Plains Research Center, Florence, SC 29502-3039, USA

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Abstract—Cotton (*Gossypium hirsutum* L.) seedlings were morphologically responsive to red (R) and far-red (FR) light (low and high FR/R photon ratios, respectively) from time of emergence. Controlled environment R and FR treatments confirmed phytochrome involvement in biomass allocation among new leaf, stem and root growth. Seedlings that received the high FR/R photon ratio developed longer and heavier stems, leaves with lower specific weights, less massive roots and higher shoot/root biomass ratios. Other cotton seedlings were grown in sunlight over different colored soils or painted panels to measure morphological effects of FR/R photon ratio in upwardly reflected light. Morphological responses to a given FR/R ratio were the same whether the reflection was from natural soil or from a painted surface. Seedlings that received the higher FR/R photon ratios in upwardly reflected light developed longer stems, leaves with lower specific weights, less massive roots and higher shoot/root biomass ratios. The potential use of colored mulches in agriculture was discussed.

INTRODUCTION

Field plant canopy interception of photosynthetic light has received considerable attention for many years. However, photomorphogenic light was only recently recognized as a regulator of photosynthate partitioning among developing parts of a growing plant and as an important factor in plant adaptation, survival and productivity in the field.

Kasperbauer (1971, 1973) noted that mid-plot and close-spaced tobacco (*Nicotiana tabacum* L.) seedlings in the field resembled plants that received more far-red light (FR)† [relative to red (R)] in controlled environments. He concluded that the FR/R photon ratio acted through the phytochrome system and was a dominant factor in distribution and use (partitioning) of photosynthate within developing plants (Kasperbauer, 1971, 1972, 1988). Holmes and Smith (1977) studied the influence of vegetation canopies on the spectral energy distribution of sunlight and related this to the function of phytochrome within such a natural environment. Smith and Hayward (1985) used specially designed growth chambers to show that differences in fluence rates of photosynthetically active light that occur in vegetative canopies can influence the morphological responses to R and FR. Casal and Smith (1988) showed that, at fluence rates which can occur within a vegetative canopy, the blue component of white light influenced phytochrome regulation of internode elongation in mustard (*Sinapis alba* L.) seedlings.

Two approaches have been used to determine whether reflected FR was the cause of stem elongation associated with closeness of other plants. One approach was to use a spectroradiometer with the light collector on a fiber optic probe to measure the spectra of light at various distances from competing plants (Kasperbauer *et al.*, 1984), and to measure morphological characteristics of plants grown at different distances from other plants (Ballare *et al.*, 1987; Kasperbauer, 1987, 1988; Kasperbauer and Karlen, 1986). In this approach, a seedling could be removed from its position in the field plot and the light collector placed where the seedling had been to determine spectra of light coming to that point from all directions. The amount of FR relative to R was highest when the seedlings were closest. The other approach involved placing light filters around seedling stems to determine morphological responses to FR and the ratio of FR relative to R photons on stem elongation (Ballare *et al.*, 1990). Both of these approaches contributed to the understanding that green seedling morphology is greatly influenced by the amount of FR reflected from other plants, and its action through the phytochrome system.

Since seedlings are morphologically responsive to FR reflected from competing plants and to FR in controlled environments, we asked whether seedlings would also be responsive to FR reflected from other objects such as soil, dead plant residue or even artificially colored surfaces. The initial experiment involved spectral measurements of light reflected from different colored soils and dead plant residues (Kasperbauer and Hunt, 1987). Other experiments showed that tomato (*Lycopersicon esculentum* L.) plants yielded more fruit when grown with red rather than black or white mulches (Decoteau *et*

*To whom correspondence should be addressed.
†*Abbreviations*: FR, far-red light; P, phytochrome; Pfr, far-red absorbing form of phytochrome; Pr, red absorbing form of phytochrome; R, red light.

al., 1989), and soybean [*Glycine max* (L.) Merr.] seedlings developed more nitrogen-fixing nodules on their roots when grown over white surfaces (Hunt *et al.*, 1989). The present study was done to test cotton (*Gossypium hirsutum* L.) seedling responsiveness to (a) high *vs* low FR/R photon ratios when photosynthetic light and temperature did not differ between R and FR treated plants, (b) upwardly reflected FR and FR/R photon ratios over different colored soils and soil covers (mulches) in a greenhouse when rhizosphere temperatures did not differ below the various soil surface colors, and (c) upwardly reflected FR and FR/R photon ratios over different colored mulches in the field.

MATERIALS AND METHODS

Plant material. Cotton (*Gossypium hirsutum* L. cv. "PD-1") plants were started from seed and grown in Norfolk loamy sand (Typic Paleudults) in all experiments. Four or five seeds were sown in each pot, or in each plant position when sown in field plots. At emergence, the seedlings were thinned to one per container, by cutting the extra plants below their cotyledons. This approach allowed selection of uniformly sized seedlings within each experiment, and it did not disrupt root growth of the remaining seedling. All photomorphogenic light treatments began at seedling emergence and continued each day for 20 days in the controlled environment and for about a month in the greenhouse and field studies. At the end of the treatment period, leaves were removed, weighed, and measured for area on a LiCor*-3100 Area Meter (LiCor Inc., Lincoln, NE). Stems were measured and weighed. Soil was washed from the roots, and the roots were weighed. Data were analyzed by the ANOVA procedure (SAS Institute, 1985) and are presented as means per plant.

Upwardly reflected light. Light reflected from the different soil-covered and painted surfaces used in greenhouse and field experiments was measured about 10 cm above those surfaces. That distance above the soil surface was selected because it was within the seedling establishment zone. Exterior paints were used in some greenhouse and all field experiments because they allowed a convenient and economical way to obtain desired reflection spectra that were suitable for small plot experiments. Measurements were taken with a LiCor-1800 Spectroradiometer (LiCor Inc., Lincoln, NE) with a remote hemispherical cosine-corrected light collector mounted on a 1.5 m fiber optic probe. The spectroradiometer was programmed to measure at 5 nm intervals from 400 to 800 nm. Incoming sunlight was measured each time reflected light measurements were taken. The reflected light values were then calculated as percentages of the 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 at time of measurement. This approach was used because field plants normally grow in sunlight with constantly changing spectral characteristics, and the working hypothesis in these studies is that a FR/R ratio higher or lower than that in incoming sunlight should signal different developmental patterns than would be obtained with the FR/R ratio in incoming sunlight. The R values were taken at 645 nm rather than 660 nm (the *in vitro* absorption peak for Pr) because the R action peak in green plants is shifted to about 645 nm by competitive absorption at 660 nm by chlorophyll (Kasperbauer *et al.*, 1963). The measurements presented in this report were taken under sunlight at solar noon ± about 1 h at different times during the experiments. Values presented in this report are means of at least five separate readings.

Controlled environment. All plants in the controlled environment experiment were grown in the same chamber for about 23 h and 50 min each day at 25°C with 12 h photosynthetic periods of cool-white fluorescent light at 500 μmol $m^{-2}s^{-1}$. At the end of the daily photosynthetic period, plants were exposed to either 5 min of R (3.6 W m^{-2} in the 600–700 nm waveband), 5 min of FR (3.6 W m^{-2} in the 700–770 nm waveband) or 5 min FR followed immediately by 5 min R at 25°C, then returned in darkness to the growth chamber for the remainder of the 12 h night. Thus all plants received the same growth environment except for the brief R and FR irradiations at the end of each day to put phytochrome predominantly in the Pfr or the Pr form, respectively, at the beginning of the night. All pots were watered with half-strength Hoagland nutrient solution (Hoagland and Arnon, 1950) twice per week throughout the experiment.

Greenhouse. Seeds were sown in 5 L pots of soil and germinated on a greenhouse bench in all of the experiments. After seedlings began to emerge, they were thinned to one per pot as described above. Pots were spaced about 60 cm apart on benches in groups of four. A styrofoam insulation panel (122 × 122 × 2 cm) with four 2.5 cm (diam) holes was placed over each group of four pots so that a seedling was centered in each hole. Some of the panel surfaces were covered with about 5 mm of the selected color of soil. Other panels were painted with exterior enamels having the reflection characteristics described below. These experimental systems allowed plants to receive upwardly reflected light from the respective surface color while root temperature differences below the different colors were minimized. Soil temperature below the insulation panels were monitored at depths of 2.5 cm at 5 min intervals and averaged each hour for 8 days. Temperatures were determined with copper-constantin thermocouples attached to a Campbell CR-7 Datalogger (Campbell Scientific, Logan, UT), as described by Hunt *et al.* (1989). Mean root temperature differences in soil under red *vs* white painted panels were less than 0.5°C. Greenhouse data are expressed as means for 8 plants per treatment.

Field. One experiment was conducted with greenhouse-germinated seedlings in pots covered with painted insulation panels as described for the greenhouse experiments. No soil covered panels were used in the field because the soil would have been removed by wind or rain. This experiment tested whether growth responses outdoors differed from those under greenhouse glass, which filtered out wavelengths shorter than about 330 nm. Shoot and root characteristics were measured as described for greenhouse potted plants.

The other field experiment involved placement of strips of black plastic horticultural mulch in rows over trickle irrigation tubes, but without insulation panels between the plastic mulch and the soil. Ten cm (diam.) holes were cut at 60 cm intervals. The mulches were painted green, red or white to test effects of mulch surface color on growth of seedlings in field plots. There were four replicates of six plants each for each color. Since the seedlings were grown directly in field plots, only shoot size was measured.

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Table 1. Cotton seedling growth and biomass distribution responses to end-of-day irradiations with 5 min red (R, low FR/R ratio), 5 min far-red (FR, high FR/R ratio), or 5 min FR followed immediately by 5 min of R (FR, R) under controlled environments

Plant characteristic	Light and FR/R ratio: R (Low ratio)	FR (High ratio)	FR, R (H, L)
Specific leaf wt. (mg/cm²)	23 a*	21 b	23 a
Stem			
Length (mm)	121 a	188 b	126 a
Hypocotyl (mm)	61 a	100 b	57 a
Wt. (mg)	1721 a	2119 b	1847 a
mg/mm	14.2 a	11.2 b	14.6 a
Root wt. (mg)	5403 a	3891 b	5298 a
Shoot/root (ratio)	0.95 a	1.27 c	1.06 b

*Values in the same row that are followed by different letters differ at the 5% level of significance.

RESULTS AND DISCUSSION

Test of seedling response to red light and far-red light in a controlled environment

Cotton seedlings responded dramatically to FR or R (high or low FR/R photon ratios, respectively) given at the end of each day (Table 1). Further, when FR was followed immediately by R, the plants responded to the color received last. Photoreversibility of the effect of FR by a brief exposure to R confirmed phytochrome involvement in the regulation of biomass distribution in these newly emerged seedlings even though photosynthetic light and temperature did not differ among plants that received the different end-of-day treatments. Seedlings that received FR (a high FR/R ratio) last each day developed lower specific leaf weights, longer and heavier stems, less massive roots and higher shoot/root biomass ratios. These observations indicate that a high FR/R ratio acts through the phytochrome system within the plant to initiate physiological events that result in partitioning a greater amount of new photosynthate to shoot growth, leaving less for new root growth.

A high FR/R photon ratio at the end of day puts a low amount of phytochrome in the FR-absorbing form (Pfr) at the beginning of the night (Borthwick, 1972; Kasperbauer *et al.*, 1964); and the Pfr/P ratio is influenced by overlapping absorbencies of Pr and Pfr at the incoming waveband of light as well as the competitive absorption by other pigments within the plant tissue (Kasperbauer *et al.*, 1963). It is not clear, however, whether a low Pfr/P ratio (the consequence of irradiation with FR) in a growing plant triggers metabolic events leading to "competition-adapted" development or whether the events occur because the Pfr/P ratio is too low to signal initiation of events leading to "sun-adapted" development. Nevertheless, the important point in the present discussion is that the phytochrome system in seedlings responds to the FR/R ratio and regulates biomass allocation within the growing plant.

Phytochrome-mediated prioritization in the distribution and use (partitioning) of photoassimilates within a growing seedling has ecological implications for survival under field conditions. That is, longer stems would increase the probability of keeping some leaves above the competition, an adaptive response that should favor survival among close spaced plants. Responsiveness of seedlings to FR (as shown in Table 1) suggests that field growth conditions other than nearness of competing plants might also affect the FR/R photon ratio sufficiently to alter partitioning and morphological development. Since plants do respond morphologically to FR/R ratio and cannot discern the source of an altered FR/R ratio, other experiments were done with cotton seedlings in sunlight over different colored soils and soil covers (mulches) that altered the amounts and ratios in reflected light while not interfering with incoming sunlight.

Reflection from colored surfaces used in greenhouse and field experiments

Characteristics of upwardly reflected light above green, red and white surfaces are summarized in Table 2. The values are expressed as percentages of reflected light relative to incoming sunlight at the same wavebands, and as FR/R ratios. Since the FR/R photon ratio in incoming sunlight varies with season, time of day and atmospheric cover, the FR/R ratio in the incoming sunlight was assigned a value of 1.00 and the ratios in reflected light are expressed relative to that value. This is a realistic approach because field plants grow in sunlight, and a reflected FR/R photon ratio that deviates from the ratio in incoming sunlight should affect seedling morphological development. A growth response to an increased FR/R ratio reflected from soil or a soil cover would be analogous to a response to an increased FR/R ratio due to FR reflection from competing plants, as demonstrated in previous studies (Ballare *et al.*, 1987; Kasperbauer *et al.*, 1984; Kasperbauer and Karlen, 1986).

The FR measurements are shown for 735 and 755 nm because 735 nm is near the absorption peak for Pfr and 755 nm is near the beginning of the FR plateau reflected by green leaves (Kasperbauer, 1987). Prolonged exposure to wavelengths up to 795 nm on the Beltsville Spectrograph resulted in FR responses in green seedlings (Kasperbauer *et al.*, 1963). It is also relevant that Vogelmann and Bjorn (1984) found higher values for FR (at 750 nm) inside fleshy leaves than at the exterior surface of those leaves, which they attributed to scattering of FR photons and little competitive absorption at 750 nm within the plant tissue. Thus, FR wave-

Table 2. Characteristics of upwardly reflected light 10 cm above different colored soils and painted surfaces used in greenhouse and field experiments

Characteristic	Soil surface color: Red	White	Panel surface color: Green	Red	White
	Percentage reflected*				
PPF† (400–700 nm)	13	36	11	16	44
R (645 nm)	22	37	10	29	45
FR (735 nm)	26	37	13	32	45
FR′ (755 nm)	27	38	19	33	44
	FR/R photon ratio in upwardly reflected light*				
FR/R	1.18	1.00	1.24	1.11	1.00
FR′/R	1.23	1.01	1.82	1.15	0.98

*Values are means of at least 5 separate readings and are expressed as percentages of incoming sunlight at the measured wavelengths, or as photon ratios in reflected light relative to 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′.
†PPF, photosynthetic photon flux.

Table 3. Shoot and root growth of cotton seedlings grown over insulation panels covered with brick-red or white soil from 13 May to 10 June in a greenhouse without supplemental lighting near Florence, SC

Plant characteristic	Soil surface color: Brick-red	White	Sig.*
Leaf			
Area (cm^2)	418	417	NS
Wt. (mg)	10148	10697	NS
mg/cm^2	24	26	*
Stem			
Length (mm)	302	277	*
Soil to 1st leaf (mm)	122	111	*
Wt. (mg)	6888	7124	NS
Root wt. (mg)	15753	18559	*
Shoot/root (wt. ratio)	1.08	0.96	*
Total plant wt. (mg)	32789	36380	*
Biomass distribution among plant parts (%)			
Leaves	31	29	NS
Stems	21	20	NS
Roots	48	51	*

*Statistical significance: *, values in the same row differ at the 5% level; NS, values are not significantly different at the 5% level.

lengths around 750, and beyond, may be more important than those near the *in vitro* Pfr absorption peak (approximately 735 nm) when regulating plant adaptive responses to prolonged exposures as occur under field conditions. Of the colors compared (Table 2), white painted surfaces reflected the most photosynthetic light but a FR/R ratio very similar to the ratio in incoming sunlight, whereas the green and red painted surfaces reflected higher FR/R ratios but only about 11 and 16%, respectively, of the photosynthetic light. As with the painted surfaces, the white soil surface reflected more photosynthetically active light and a FR/R ratio similar to that in incoming sunlight, while the brick-red soil reflected about 13% of the photosynthetic light and a FR/R ratio of about 1.2 (see Table 2).

Seedling responses to spectrum of upwardly reflected light in a greenhouse

Because of earlier studies with prolonged FR treatments on the Beltsville Spectrograph (Kasperbauer *et al.*, 1963) as well as investigations of plant responses to FR reflected from competing plants under field conditions (Kasperbauer, 1987; Kasperbauer *et al.*, 1984), we hypothesized that even small differences in the FR/R ratio over the various colored soils, plant residues or artificially colored surfaces could have significant impact on cotton seedling morphology. If true, a higher FR/R ratio (as found over the green or red surfaces, see Table 2) should be sensed the same as competition from other plants and signal the growing plant to adapt to this perceived competition by developing longer stems, leaves with lower specific weights, and perhaps smaller root systems and higher shoot/root biomass ratios.

Soil-covered insulation panels. Shoot and root characteristics of plants grown in sunlight over brick-red or white soil-covered insulation panels were compared (Table 3). Plants grown over the brick-red surfaces (higher reflected FR/R ratios) had leaves with lower specific weights, longer stems, less root biomass, and higher shoot/root biomass ratios. This response supports our hypothesis that photosynthate partitioning within plants growing in sunlight can be altered by the FR/R ratio even though the altered ratio is not caused by reflection of FR from other nearby plants. Awareness that seedlings can respond morphologically to natural differences in color of soil can help to explain why plant productivity with conservation tillage (dead plant residue from a previous crop left on the soil surface) *vs* conventional tillage varies among geographic areas which have different colored soils (Campbell *et al.*, 1984; Phillips *et al.*, 1980).

We hypothesized that plants grown in sunlight should respond the same to a given spectrum of upwardly reflected light whether the reflecting surface was natural soil or an artificially colored surface. To test this concept, exterior paints were spread on insulation panels to provide reflected light spectra similar to those over red or white soil.

Painted insulation panels. Shoot and root characteristics differed significantly on plants grown in sunlight over red *vs* white painted insulation panels in a greenhouse (Table 4). As with plants grown

Table 4. Shoot and root growth of cotton seedlings grown over insulation panels with red or white painted surfaces in October in a greenhouse without supplemental lighting near Florence, SC

	Panel surface color		
Plant characteristic	Red	White	Sig.*
Leaf			
Area (cm^2)	372	319	*
Wt (mg)	8640	8445	NS
mg/cm^2	23	26	*
Stem			
Length (mm)	289	228	*
Soil to 1st leaf (mm)	168	132	*
Wt. (mg)	6290	5619	NS
Root wt. (mg)	7425	9005	*
Shoot/root (ratio)	2.01	1.56	*
Total plant wt. (mg)	22355	23069	NS
Biomass distribution among plant parts (%)			
Leaves	39	37	NS
Stems	28	24	*
Roots	33	39	*

*Statistical significance: *, values in the same row differ at the 5% level; NS, values are not significantly different at the 5% level.

over brick-red *vs* white soils, those grown over the red surfaces received higher FR/R ratios in upwardly reflected light and they developed leaves with lower specific weights, longer stems, less root biomass and higher shoot/root biomass ratios.

These plant responses to soil surface color demonstrated that spectral composition of light reflected up to seedlings from different colored soils (and soil covers) can significantly affect morphological development under greenhouse conditions. Additional studies were done outdoors in full incoming sunlight to determine whether greenhouse glass filtering of incoming sunlight contributed to the morphological responses of cotton seedlings, or if the same growth pattern would be obtained outdoors.

Seedling responses to spectrum of upwardly reflected light outdoors

Potted cotton seedlings grown outdoors with red- or white-painted insulation panels exhibited essentially the same trends in stem elongation and shoot/root biomass ratios as were observed in the greenhouse, indicating that the waveband of light filtered out by greenhouse glass was not a dominant factor. Also, the pattern of shoot growth in response to spectrum of upwardly reflected light was very similar when surface-painted plastic sheets were used with (Table 5) or without (Table 6) insulation panels placed below the green, red, or white surface-colored plastic. That is, plants grown over the green or red surfaces received higher reflected FR/R ratios (see Table 2) and developed larger shoots than those grown with white.

Table 5. Shoot and root growth of potted cotton seedlings grown outdoors over insulation panels with green, red or white painted surfaces from 29 May to 21 June near Florence, SC

	Panel surface color		
Plant characteristic	Green	Red	White
Stem length (mm)	148 a*	135 ab	111 b
Shoot wt. (mg)	11784 a	10366 ab	9679 b
Root wt. (mg)	11076 a	10512 a	11162 a
Total plant wt. (mg)	22860 a	20878 b	20841 b
Shoot/root (ratio)	1.06 a	0.99 a	0.87 b

*Values in the same row followed by different letters differ at the 5% level of significance.

When cotton seedlings were grown in soil in field plots that were covered with surface-painted plastic sheets (Table 6), plant growth responses were as predicted by the controlled environment study (Table 1), the quantities and ratios of reflected light (Table 2), and the responses to upwardly reflected light over different colored surfaces in the greenhouse (Tables 3 and 4). Plants grown over the green surface (which reflected the highest FR/R ratio) had the longest stems and those over white had the shortest stems (Table 6). These results are consistent with the hypothesis that a FR/R ratio higher than that in incoming sunlight favors shoot growth, when soil moisture and nutrients are adequate.

In conclusion, cotton seedling stem elongation is very responsive to the FR/R ratio, which acts through the phytochrome system within the plant. In nature, seedlings sense FR and a higher FR/R ratio as an indication of competition from other plants because green leaves of the competing plants reflect FR, and the FR/R photon ratio received by a field grown plant is related to the size, number, nearness and even heliotropic orientation of competing leaves. The adaptive response to a higher FR/R ratio is to allocate a higher proportion of new photosynthate to new stem growth, leaving less for

Table 6. Shoot length of cotton plants grown outdoors in sunlight in field plots covered with surface-painted plastic mulch near Florence, SC

	Mulch surface color		
Weeks after emergence	Green	Red	White
	Plant ht (mm)		
5	463 a*	434 b	331 c
8	842 a	784 b	689 c

*Values in the same row followed by different letters differ at the 5% level of significance.

new root growth. This results in a higher shoot/root biomass ratio. Seedlings are so sensitive that the subtle differences in FR/R ratio in upwardly reflected light over different colored soils or soil covers (mulches) can also act through the phytochrome system and regulate adaptive morphogenesis in response to the ratio. A FR/R ratio greater than the ratio in incoming sunlight is sensed by the phytochrome system as a signal of nearby plants and favors shoot growth, whereas a lower ratio is hypothesized to favor root growth. Since mulches are widely used to control weeds and to conserve soil and water in production of high value crops, use of mulches with surface colors that reflect predetermined FR/R ratios offers the potential to manage phytochrome-regulated photosynthate partitioning to improve the quantity and quality of field-grown plant products at little added cost to the grower while maintaining the desired soil and water conserving characteristics of mulch.

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