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Far-Red Light Reflection from Green Leaves and Effects on Phytochrome-Mediated Assimilate Partitioning under Field Conditions

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MICHAEL J. KASPERBAUER
United States Department of Agriculture, Agricultural Research Service, Coastal Plains Soil and Water Conservation Research Center, P.O. Box 3039, Florence, South Carolina 29502-3039

ABSTRACT

The influence of plant spacing and row orientation on spectral distribution of light received by growing soybean (*Gylcine max* [L.] Merr.) plants was measured under field conditions. Light absorption, reflection and transmission of individual leaves showed that most of the blue and red was absorbed while most of the far-red was either reflected or transmitted. Plants growing in the field received different ratios of far-red relative to red, depending on nearness and/or orientation of other vegetation. Plants grown in close-spaced rows, or high population densities, received higher far-red/red ratios than did those grown in wide rows, or sparse populations. Heliotropic movements of the leaves also contributed to the far-red reflection patterns associated with row orientation. Under field conditions, differences in far-red/red ratios associated with nearness of competing vegetation became more pronounced with low solar angle near the end of the day. Plants exposed to far-red for 5 minutes at the end of each day in controlled environments, and those grown in close-spaced rows in the field, developed longer internodes and fewer branches. Red, far-red photoreversibility in the controlled environment study indicated involvement of phytochrome. Dry matter partitioning among plant components in the field was related to far-red/red light ratio received during growth and development.

Plants of the same genotype frequently differ in phenotypic development when grown in crowded relative to sparse populations. It is apparent that each plant is genetically programmed for a number of alternate developmental patterns and that expression depends on the environmental combination that exists during plant growth and development (1, 9, 17). Therefore, management of natural regulation of plant development might improve yield and/or quality of crop plants and plant products.

In a recent study, Hunt *et al.* (8) found that soybean yields on sandy soils with low water-holding capacity were usually higher from north-south rows when there was no water stress (irrigated) during growth and development, and higher from east-west rows if there was intermittent water stress. A possible explanation is that row orientation in some way influenced the plant shoot/root ratio, and this, in turn, affected response to intermittent water stress. It appears that (a) there is a distinct environmental difference associated with change in plant spacing and row orientation, (b) plants contain a sensor of that environmental difference, and (c) the sensor within the plant is capable of regulating assimilate partitioning among shoots and roots during plant growth and development. Perhaps the spectral distribution of light is involved. The objectives of the present study were to measure (a) absorption, transmission, and reflection of FR[1] and visible light by a single leaf, (b) spectral distribution of light received by plants growing in various row spacings and orientations, and (c) influence of row spacing and orientation on plant growth and development.

MATERIALS AND METHODS

Soybean (*Glycine max* [L.] Merr. cv Coker 338) plants were used in field and controlled-environment studies.

Field. Plants were grown on irrigated plots of Norfolk loamy sand (Typic Paleudults) at the Coastal Plains Soil and Water Conservation Research Center, Florence, SC. Plots were overseeded and thinned to 20 plants per m of row. Spacing between rows was an experimental variable. Plots were fertilized and irrigated as needed to avoid nutrient and water stress.

Spectral distributions of incoming radiation received by leaves near the top of the canopies were measured at 5-nm intervals between 400 and 850 nm with a LiCor[2] Spectroradiometer LI-1800 equipped with a remote light collector on a fiber optic probe. A reference spectrum was obtained by measuring direct solar radiation. Spectral irradiances at 735 and 645 nm were used to calculate the FR/R ratios. These values were used because they approach the peaks for phytochrome action spectra in green plants; 645 nm was used instead of 660 nm because Chl competition for light at 660 nm (the phytochrome *in vitro* peak) shifts the phytochrome action peak to about 645 nm in green plants (10). Values for absorption by, transmission through, and reflection from single leaves were obtained using a LiCor-1800-12 integrating sphere.

The changing FR/R ratios in direct sunlight were measured during the last 2 h of a cloudless day. The spectroradiometer was placed on a table away from vegetation in an open field, and programmed to automatically determine the FR/R ratio at 3-min intervals. During the 2-h period, photosynthetic photon flux decreased from 1150 to less than 1 μmol m^{-2} s^{-1}.

Data on plant characteristics were collected during vegetative growth and after seed were ripe. Five-plant samples (per replicate) were taken during growth. Components of the plants were measured and weighed to determine row orientation and spacing effects during growth on plant morphogenesis and dry matter distribution when nutrients and water were not limiting. One-m

[1] Abbreviations: FR, far-red light; R, red light; P_r, red-absorbing form of phytochrome; P_{fr}, far-red-absorbing form of phytochrome.

[2] Mention of trademark, proprietary product, or vendor anywhere in this paper does not constitute a guarantee or warranty of the product by the United States Department of Agriculture and does not imply its approval to the exclusion of other products or vendors that may also be suitable.

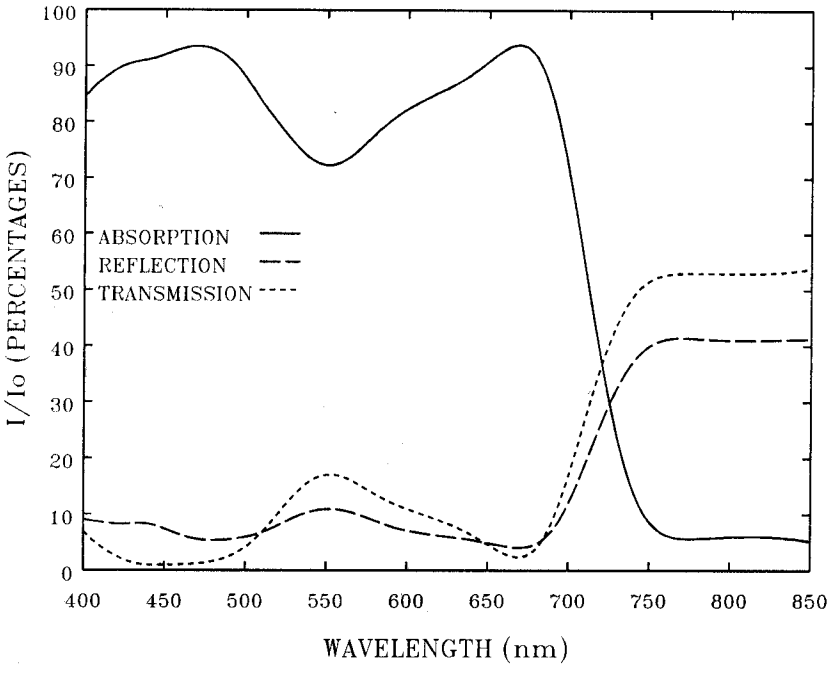

FIG. 1. Absorption, transmission, and reflection of a typical soybean leaf. I/I_o refers to radiation absorbed, transmitted, and reflected at 5-nm intervals relative to incident radiation at the same wavelengths.

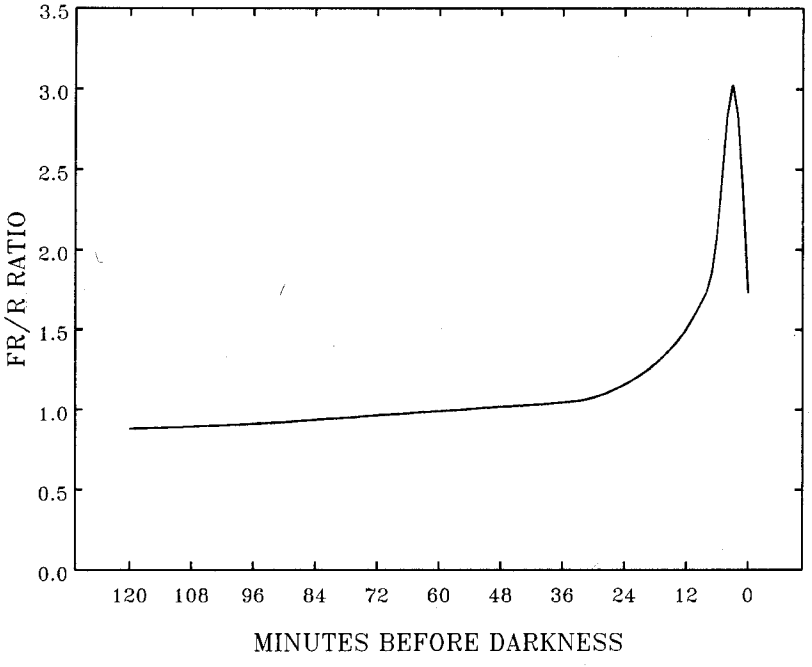

FIG. 2. FR/R ratios in sunlight taken at 3-min intervals for the last 2 h of a cloudless day near Florence, SC.

row samples (*i.e.* 20 consecutive plants per replicate) were taken at harvest to measure effects on seed and straw. There were five replicates at each sampling date.

Controlled Environments. Seedlings were started and grown in a vermiculite-potting soil (3:1, v/v) mixture; 3-L pots were used. Five seeds were sown per pot. Seeds were germinated at 28°C. After emergence, the seedlings were thinned to two per pot. All pots were watered with half-strength Hoagland nutrient solution (5) twice per week throughout the experiment. All plants received the same treatment except for R and FR at the end of each day to put phytochrome predominantly in the P_{fr} or the P_r form, respectively, at the beginning of the night.

All plants were grown in the same controlled-environment chamber at 25°C with 12-h d of cool-white fluorescent light at 520 μmol m^{-2} s^{-1}. At the end of the daily light period, plants were exposed to either 5 min of R (3.6 W m^{-2} in the 600–700 nm waveband) or to 5 min of FR (3.6 W m^{-2} in the 700–770 nm waveband) at 25°C, then returned in darkness to the growth chamber for the remainder of the 12-h night. To test photoreversibility, another set received 5 min of FR followed immediately by 5 min of R light. The R radiation unit consisted of two layers of red cellophane under a bank of cool-white fluorescent lamps; whereas, the FR unit consisted of two layers of red and two of dark blue cellophane under internal-reflector, incandescent-filament lamps, as used in earlier studies (11). Daily R and FR treatments began when seedlings reached the unifoliolate leaf stage. Representative plants were photographed after 9 d of treatment, and vegetative samples were taken after 20 d.

RESULTS AND DISCUSSION

Light Absorption, Reflection, and Transmission of a Single Leaf. Light absorption, reflection, and transmission of a typical

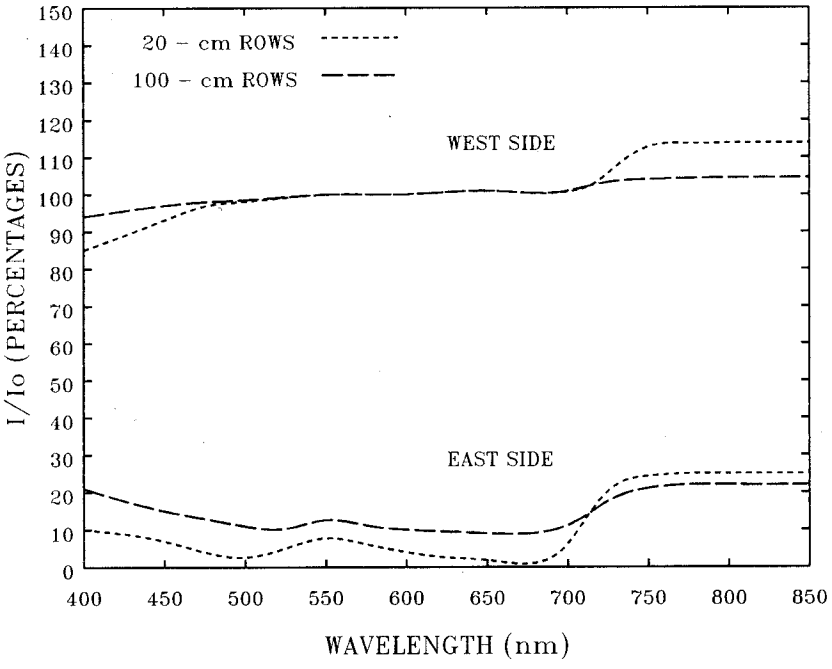

FIG. 3. Spectral distribution of light received in mid-afternoon by soybean plants growing in close- and wide-spaced north-south rows. The detector was in sunlight on the west side and in shade on the east side of the row. I/I_o refers to the ratio of light measured at the indicated point relative to that measured in direct sunlight at the same wavelength. Measurements were taken at 5-nm intervals.

Table I. *FR/R Ratios in Direct Sunlight and at Surface of Upper Canopy of 6-Week-Old Soybean Plants in 20- and 100-cm North-South Rows Near Florence, SC August 29, 1984*

Time	FR/R				
	Direct sunlight	West side		East side	
		20 cm	100 cm	20 cm	100 cm
h			*ratios*		
1030	0.83	1.51	0.96	1.34	0.94
1310	0.82	1.30	0.91	1.48	0.97
1730	0.89	1.00	0.96	8.91	1.99

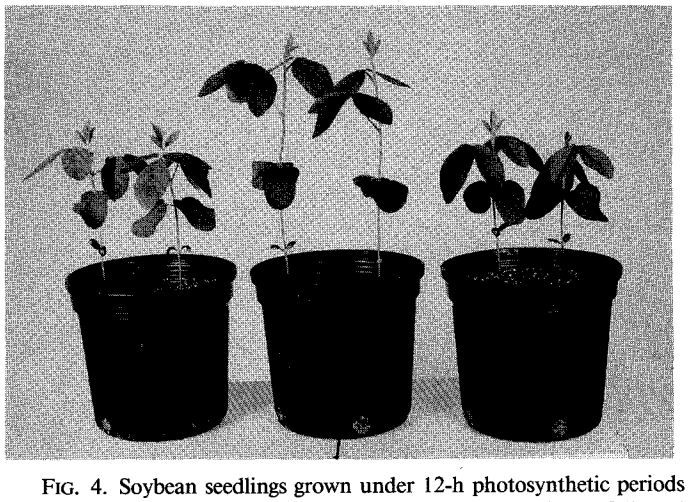

FIG. 4. Soybean seedlings grown under 12-h photosynthetic periods that ended with 5 min R (left), 5 min FR (middle), or 5 min FR followed immediately by 5 min R light (right) each day for 9 consecutive days. The treatments began when plants were in the unifoliolate stage.

soybean leaf are shown in Figure 1. The reflection and transmission characteristics of individual leaves (and different areas of the same leaf) varied somewhat due to leaf veination and other structural differences. However, large R absorption and small FR absorption were consistent among green soybean leaves. Transmission of light through the soybean leaves was similar to that shown for tobacco in an earlier report (9). As discussed in that report, light transmitted through green leaves influences the light spectrum within and below the canopy. In addition to light transmitted through leaves to the soil surface, light transmitted through "sun tracking" leaves near the end of the day may influence light spectra received by adjacent plants.

While light transmitted through leaves has received attention relative to its effects on suppression of weed seed germination and other shading responses (3, 4, 6, 7, 9, 15, 16), light reflected from the leaves may be even more important in adaptation of a plant to competition from other plants. Because of high absorption by carotenoids and Chl from 400 to 700 nm and relatively little absorption of wavelengths beyond 700 nm (Fig. 1), it is reasonable to hypothesize that this may be involved in a mechanism that can sense competition from other plants under field conditions. The ratio of FR relative to R in light reflected from a green leaf would certainly differ from that in direct sunlight. Further, the spectral balance of reflected light would very likely be influenced by the spectral balance of sunlight (which changes with diurnal changes in solar angle, Fig. 2), the number and size of reflecting leaves, the distance from the reflecting leaves, and even the heliotropic movements of the leaves. All of these factors might contribute to plant physiological responses to light spectrum when the plants are grown in different plant populations, row spacings, and even row orientations.

Reflection from Other Plants. Spectral distributions of light received by plants growing in north-south *versus* east-west rows changed with solar angle and size of competing plants. There were larger FR/R ratio differences between the east and west sides of north-south rows than between the north and south sides of east-west rows. Within-row differences were less pronounced than those between rows. The FR/R ratios near the top of growing plants averaged about 1.15 in the north-south rows and about 1.05 in the east-west rows when the FR/R ratios taken at about 0900, 1200, and 1600 h were averaged from north, south, east, and west for both north-south and east-west rows. The important point is that higher FR/R ratios were detected for plants growing in the north-south rows. Heliotropic movement of leaves appeared to be involved in the differences in FR/R ratios especially at low solar angles.

Shifts in spectral distributions of light received near the top of

Table II. *Percentages of Dry Matter Partitioned among Shoots and Roots of Soybean Seedlings Grown in Controlled Environment with End-of-Day R or FR Treatment Each Day for 20 Consecutive Days*

Daily irradiations with R and FR were for 5 min. The FR + R treatment received 5 min FR followed immediately by 5 min R. Plants were returned in darkness to the dark controlled environment chamber.

End-of-Day Light	Dry Matter Distribution					
	Shoots			Roots		
	Leaf blades	Stems + petioles	(Total)	Roots	Nodules	(Total)
			%			
R	43.9	23.6	(67.5)	30.1	2.4	(32.5)
FR	43.6	33.2	(76.8)	21.3	1.9	(23.2)
FR + R	43.4	22.8	(66.2)	31.3	2.5	(33.8)

Table III. *Shoot Characteristics of 5-Week-Old Soybean Plants Grown in North-South (N-S) versus East-West (E-W) Rows in Irrigated Loamy Sand in Field Plots*

Plant Characteristics	Row Orientation	
	N-S	E-W
Stem length (cm)	34.8 ± 0.6[a]	32.4 ± 0.5
Nodes/stem	8.1 ± 0.1	8.2 ± 0.1
Branches/plant	1.8 ± 0.4	3.0 ± 0.2

[a] Values were means ± SE.

Table IV. *Row Orientation Effects on Dry Matter Distribution in Shoots of Late-Sown Soybean Plants Grown to Ripeness in North-South (N-S) versus East-West (E-W) Rows in Irrigated Loamy Sand Field Plots*

Rows were [illegible]n apart and samples included 20 consecutive plants (1-m of row) from each of 5 rows. Leaves had fallen and are not included.

Plant Characteristics	Row Orientation	
	N-S	E-W
	g dry matter/1-m row	
Seed	158.2 ± 7.8[a]	142.8 ± 7.5
Pods	58.2 ± 3.0	53.0 ± 4.0
Stems	43.8 ± 1.9	40.8 ± 3.2
Seed/straw (ratio)	1.55	1.52

[a] Values are means ± SE.

Table V. *Row Spacing Effects on FR/R Ratio and Shoot Characteristics of 6-Week-Old Soybean Plants Growing in North-South Rows in Irrigated Loamy Sand Field Plots*

Parameter	Row Spacing (cm)			
	18	35	50	100
FR/R ratio of incoming light near top of plant in midmorning[a]				
East side	1.08	1.05	0.96	0.89
West side	3.45	2.99	2.11	1.41
Shoot characteristic[b]				
Stem length (cm)	45.7 ± 0.8	44.6 ± 0.7	41.0 ± 0.9	35.9 ± 0.8
Nodes/stem	9.1 ± 0.2	9.4 ± 0.1	9.5 ± 0.2	9.3 ± 0.2
Branches/plant	0.2 ± 0.1	0.6 ± 0.2	1.9 ± 0.3	3.6 ± 0.2

[a] FR/R ratio in direct sunlight was 0.88 at 0900 August 28, 1984, immediately before ratios were measured in plant canopies near Florence, SC. [b] Values are means ± SE.

growing soybean plants in north-south rows are shown in Figure 3. The spectral shifts relative to the spectrum of direct sunlight are emphasized because plants are adapted to sunlight. It is hypothesized that spectral deviations from natural sunlight signal

Table VI. *Row Spacing Effects on Plant Height and Dry Matter Distribution in Shoots of Early Sown Soybean Plants grown in North-South Rows in Irrigated Loamy Sand Field Plots*

Data collected after seed ripened in the field.

Plant Characteristics	Row Spacing (cm)			
	18	35	50	100
Stem length (cm)	116 ± 3[a]	106 ± 4	97 ± 3	91 ± 3
Dry matter distribution in shoots (per 1-m row)				
Seed (g)	56 ± 5	100 ± 9	136 ± 9	235 ± 10
Pods (g)	23 ± 3	36 ± 4	48 ± 3	88 ± 6
Stems (g)	59 ± 4	96 ± 5	141 ± 8	172 ± 7
Seed/straw (ratio)	0.68	0.76	0.72	0.90

[a] Values are means ± SE.

the plant to adjust physiological processes for better adaptation, and survival, under the modified light environment. The data (Table I) clearly show that the FR/R ratio received by growing plants is influenced by the nearness of competing vegetation and by time of day (solar angle). That is, the FR/R ratio in sunlight increases as the day progresses toward sunset (Fig. 2), and the difference in ratio received by growing plants is magnified by the amount and nearness of competing vegetation. Therefore, the difference in FR/R ratio of light associated with increased population density increases rapidly near the end of the day. It is apparent from work in controlled environments that the relative amounts of R and FR (especially that received at the end of the day) influence many aspects of plant development (1, 2, 17) including chloroplast ultrastructure and carbohydrate partitioning at the cellular level (11), photosynthetic efficiency (13), and concentrations of various metabolites (14).

R and FR Photoreversible Effects. When other factors were held constant under controlled environments, soybean seedlings responded to the FR/R ratio received at the end of the photosynthetic period (Fig. 4). The fact that the plants responded to R and FR and that effects of FR were reversed by R supports the hypothesis that phytochrome is involved in the environment-sensing mechanism that regulates photosynthate partitioning. In addition to having shorter internodes (Fig. 4), plants that received R last each day (*i.e.* a low FR/R ratio) initiated axillary shoots (branches) that became evident after about 12 d (not yet evident at 9 d in Fig. 4). This is analogous to light-mediated regulation of tillering in *Triticum aestivum* (12). Under controlled environments, R and FR acted through the phytochrome system of the seedlings to regulate partitioning among shoots and roots (Table II). Thus, it is reasonable to expect that under field conditions, partitioning and plant developmental patterns would differ with row spacing and orientation patterns that influence the FR/R ratio, even before decreased photosynthetic photon flux becomes

a dominant factor.

Field Plant Growth and Development. *North-South versus East-West Rows.* Characteristics of irrigated soybean plants after 5 weeks of growth in north-south *versus* east-west rows are shown in Table III. Without water stress, plants grown in north-south rows had slightly longer internodes and had initiated fewer branches. These plants received slightly higher FR/R ratios, and observations were consistent with (but less pronounced than) the controlled environment R and FR responses (Fig. 4; Table II). That is, a slightly higher FR/R ratio should contribute to more photosynthate partitioned to shoots and developing seed and less partitioned to roots.

Plant characteristics at harvest are shown in Table IV. With identical plant spacings and no water stress, shoots of plants that grew in north-south rows were heavier and produced more seed, probably at the expense of roots (which presumably was not critical when there was no water or nutrient stress). Awareness that row orientation can influence yield (8) when other factors are favorable may become important in irrigation scheduling and other aspects of crop plant production efficiency.

Spacing of North-South Rows. Characteristics of irrigated soybean plants grown for 6 weeks in variously spaced north-south rows are shown in Table V. Plants in close-spaced rows received higher FR/R ratios during growth, and developed longer internodes and fewer branches. At harvest, close-spaced plants were taller, had fewer pods and seeds per plant, and a lower seed/straw ratio (Table VI), indicating that the trends developed during seedling growth continued and influenced allocation of dry matter to seeds and stems. Of course, genotype and seasonal changes in daylength influence time of flowering and plant size, but spectral shifts (especially the FR/R ratio) associated with population densities clearly play a major role in individual plant development.

According to the concept presented in this paper, seedlings should be especially sensitive to the FR/R ratio under field conditions because failure to respond to competition from other plants could result in competitive disadvantage and elimination. Thus, seedlings in a crowded population receive more FR and develop fewer branches and longer internodes, which allows them to keep some leaves in photosynthetic light above competing plants. From a survival standpoint, partitioning more photosynthate to stem growth rather than to branches and root growth seems realistic if the plant is growing in a high population. However, if there is no competition from other plants, survival of the species could best be served by developing more branches (with more flowers and seed) and a larger root system to support development of this seed. It is apparent that developmental responses to plant spacing and row orientation involve this same light-sensing, growth-regulating mechanism. Also, this same regulatory system can explain why plants branch (or tiller) into within-row space to 'compensate' for missing plants.

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