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Plant Spacing and Reflected Far-Red Light Effects on Phytochrome-Regulated Photosynthate Allocation in Corn Seedlings

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ABSTRACT

Allocation of photosynthate among leaves, stems, and roots is critical in seedling establishment. Corn (*Zea mays* L.) seedlings were grown in different spacing patterns in a field and with different reflected far-red (FR) to red (R) light ratios to test the effects of a modified FR/R ratio on photoassimilate allocation. Green leaves absorbed most of the R and reflected much of the FR. Therefore, close-spaced plants received more reflected FR and higher FR/R ratios. Seedlings that received the higher FR/R ratios developed longer and narrower leaves, longer stems, and less massive roots. Stem elongation was an early response to increased FR/R ratio even though light did not impinge directly on the stems, which were initially at or below the soil surface and covered by several layers of leaves. Row orientation did not significantly alter FR/R ratio or seedling morphology because corn leaves are not heliotropic and did not function as directional FR reflectors, as was observed for soybean [*Glycine max* (L.) Merr.] in a previous study. An increase in the FR/R ratio reflected up to seedlings from the soil surface also resulted in increased shoot size and shoot/root biomass ratio. Early morphological responses of corn seedlings to FR/R ratio in reflected light are relevant to seedling establishment and are not dependent on the cause of the altered ratio.

PHOTOSYNTHESIS and the allocation of photosynthate are both important for seedling survival, growth, and eventual productivity in a plant-soil-water-light management system. Canopy interception of photosynthetically active light has received considerable attention for many years (22). However, less emphasis has been given to allocation of photoassimilates among the developing leaves, stems, and roots. Research with field-grown dicotyledonous plants of several species has shown that photomorphogenic light [primarily the ratio of far-red (FR) relative to red (R)] is influenced by FR reflected from competing plants, and that the FR/R ratio can act through phytochrome within the growing plant to regulate partitioning and morphological adaptation (1, 2, 3, 4, 10, 11, 17).

Studies with soybean and tobacco (*Nicotiana tabacum* L.) have shown that the FR/R ratio received during growth of a leaf can affect its shape, thickness, stomatal frequency, chlorophyll concentration, chloroplast structure, and photosynthetic efficiency (14, 15, 19). Similarly, elongation of stem internodes of dicotyledonous plants (such as soybean and tobacco) was influenced by the FR/R ratio received while the internodes were still capable of elongating (6, 9, 17).

A field study conducted in 1983 revealed that soybean plants in north-south rows received more FR reflected from plants in adjacent rows, especially near the beginning and end of day (17). This response was attributed to heliotropic movement of the soybean leaves which caused them to be directional reflectors of FR as the leaves faced the sun at low solar angles, and they reflected FR to the adjacent row. A higher FR/R ratio resulted in longer stems and fewer lateral branches (10). In those studies, both leaves and stems received the altered FR/R ratio.

In the spring of 1984, we found that nearness of wheat (*Triticum aestivum* L.) seedlings influenced the amount of FR reflected to competing seedlings, and that an increased FR/R ratio resulted in longer leaves and development of fewer tillers (18). This response to increased FR/R ratio by wheat seedlings was consistent with altered leaf shape and suppressed basal branching responses to increased FR received by tobacco and soybean seedlings (9, 15, 17). The leaf-shaped and basal-branching responses suggest that a similar competition-sensing and growth-regulating mechanism (11) is present in wheat, tobacco, and soybean seedlings. However, we did not dissect any of the wheat seedlings to examine effects of FR/R ratio on early elongation of stem internodes, which were at or below soil level and surrounded by several layers of leaves. The present study was done with another cereal crop, corn, to evaluate (i) relationships among plant spacing, reflected FR, FR/R ratio, and biomass distribution among leaves, stems, and roots of field-grown seedlings before mutual shading became a limiting factor in photosynthesis; (ii) effects of north-south (N-S) versus east-west (E-W) row orientation on FR/R ratio and seedling growth characteristics; and (iii) morphological effects of an altered FR/R ratio when the alteration was not due to closeness of competing plants.

MATERIALS AND METHODS

Plants were grown in Norfolk loamy sand (fine-loamy, siliceous, thermic Typic Paleudult) near Florence, SC, in all of the experiments. Three or four seeds were sown in each container, or in each plant position in the field. At emergence, the seedlings were thinned to one per container, or field position, by cutting the extra seedlings below the soil line. This procedure allowed selection of uniformly sized seedlings within each experiment, and roots of the remaining seedlings were not disrupted. The procedure also allowed photomorphogenic light treatments to begin at time of emergence, whether the light variable was reflected from different spaced plants in a field or reflected up from different colored surfaces located below equally-spaced plants.

The spectrum of light reflected from the surface of a typical leaf on a 5-wk-old corn seedling was measured with a LI-COR-1800-12 Integrating Sphere (LI-COR Inc., Lincoln, NE)[1].

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[1] Mention of a trademark or product does not constitute a guarantee or warranty of the product by the USDA and does not imply its approval to the exclusion of other products or vendors that may also be suitable.

Abbreviations: E-W, east-west row orientation; FR, far-red light; N-S, north-south row orientation; PPF, photosynthetic photon flux; R, red light.

Percentages of light reflected at each measured wavelength (at 5-nm intervals from 400-800 nm) were calculated relative to the quantity of incoming light at the same wavelengths.

Field Plant Spacing and Row Orientation

Seeds were sown in three equidistant spacings (30 by 30 cm, 60 by 60 cm, and 120 by 120 cm) in irrigated field plots on 2 May 1985, and 10 April 1986. There were two plots for each plant spacing each year. Plot dimensions were 12 by 4 m for the 30- by 30-cm plant spacing, 18 by 6 m for the 60- by 60-cm spacing, and 30 by 10 m for the 120- by 120-cm spacing. One plot of each spacing had its longest dimension in the N-S direction. The other plot had its longest dimension in the E-W direction. The same plot layout was used in 1985 and 1986. Each year the seedlings were thinned to one per hill soon after emergence, as described above.

In order to test effects of nearness of other corn seedlings on shoot/root biomass relationships, the 1986 study included some seedlings that were germinated and grown in 10-cm (diam) by 45-cm polyvinyl chloride cylinders that were filled with soil and embedded in the field plots. The soil used in the cylinders was taken from an adjacent plot, thoroughly mixed, and screened through a 2-mm sieve to remove any old roots and other plant residue before adding an equal volume to each of the 30 cylinders. Five cylinders were embedded in each of the two plots in each of the three plant spacings. The soil level in each cylinder was the same as that of the surrounding soil. No embedded cylinder was adjacent to another embedded cylinder. This procedure was used so that roots could be recovered from plants grown in the different spacings after growth in the same volume of the same thoroughly mixed soil.

Other plants were sown in rows that were 75 cm apart and orientated N-S or E-W on 30 April 1985. Rows were 30 m long and there were 10 rows in each direction, adjacent to the spaced plots described above. Soon after emergence the plants were thinned to about 25 cm apart within the N-S and E-W rows. This allowed study of row orientation effects with constant plant populations. The experiment was repeated in 1986.

Spectral measurements were taken of light coming to upper leaves of the 4-wk-old seedlings in the spacing and row orientation plots at about 0830 h eastern daylight time (about 4.5 h before solar noon) on 5 June 1985. The light spectra were measured at 5-nm intervals from 400 to 800 nm with a LI-COR-1800 Spectroradiometer equipped with a remote, hemispherical, cosine-corrected light collector on a 1.5-m fiber optic probe. The light collector was held near the top of a randomly selected plant and aimed (parallel to the soil surface) at the upper leaves of the adjacent plant to the N, S, E, and W. Duplicate scans were taken at each measurement position. The same sequence was followed with two randomly selected plants in each of the three spacings and the two row orientations. The spectrum of incoming sunlight was measured by holding the light collector 2 m above the soil surface and aiming it at the sun. Spectra of light coming to the seedlings were calculated as the percentages (at each measured wavelength) of incoming sunlight. Additional scans were taken about 4.5 h after solar noon on the same date.

Ten plants were randomly selected and sampled (five plants from each of the two plots) from each of the three plant spacings and from the two row orientations about five weeks after emergence each year. Only above-ground parts were sampled from plants grown directly in the field soil. Length and width of the largest leaf blade per plant were measured. All leaves per plant were removed and separated into blades and sheaths. Leaf blade area per plant was measured on a LI-COR-3100 Area Meter. Stems were measured. Plant parts were freeze-dried and weighed. Data from the 2-yr study were analyzed by analyses of variance (ANOVA) and least significant difference (LSD) as outlined by the SAS Institute (23).

Plants that were grown in the cylinders embedded in the soil were cut at the soil surface three weeks after emergence. Roots were washed, and both shoots and roots were freeze-dried and weighed. This allowed us to determine effects of nearness of competing plants on shoot/root biomass ratio when all plants in all spacings had the same volume of the same soil mixture.

Different FR/R Ratios in Upwardly Reflected Light

Seeds were sown in 3-L pots of soil on 4 August and placed 60 cm apart in groups of four on greenhouse benches without supplemental lighting. As with the cylinder-grown plants in the field, soil from a field plot was screened through a 2-mm sieve to remove old roots, and it was thoroughly mixed before equal amounts were added to each of the pots. A styrofoam insulation panel (122 by 122 by 2 cm) with four 2.5-cm (diam) holes was placed over each group of four pots so that an emerging seedling was centered in each hole. The upper surfaces of two of the insulation panels were covered with about 1 cm of brick-red soil to give a higher reflected FR/R ratio than was present in incoming sunlight. Two were covered with gray-white soil to give the same FR/R ratio in reflected light as in incoming light. One red and one white panel were on one table and the other of each color was on the adjacent table. Similarly, two panels were painted red and two were painted white. Different colored soils and paints over insulation panels were used to test the hypothesis that an altered FR/R ratio was more influential than the surface that reflected the altered ratio. In this experimental system, each seedling emerged and began shoot growth 60 cm from the nearest seedling, causing the equally spaced seedlings to be exposed to different FR/R ratios in upwardly reflected light from time of emergence. Spectra of upwardly reflected light were measured 10 cm above the respective surfaces with a LI-COR-1800 Spectroradiometer with a remote hemispherical cosine-corrected light collector mounted on a 1.5-m fiber optic probe. The spectra of upwardly reflected light were measured 10 cm above the respective colors because this was in the seedling establishment zone. The amount of light reflected at each measured wavelength (at 5-nm intervals from 400–740 nm) was expressed as a percentage of incoming light at the same wavelength. The reflected photosynthetic light (400–700 nm) was expressed as a percentage of incoming sunlight in the same waveband. The R and FR values were measured at 645 $\pm$ 5 nm and 735 $\pm$ 5 nm because these wavebands cover the action peaks for the R-absorbing and FR-absorbing forms of phytochrome, respectively, in green plants (12, 13). The insulation panels were used in order to minimize differences in rhizosphere temperatures below the red or white surface colors, while allowing different FR/R ratios to be reflected up to the seedlings. Temperatures were determined with copper-constantin thermocouples attached to a Campbell CR-7 Datalogger (Campbell Scientific, Logan, UT) as described by Hunt et al. (8). Mean root temperature difference in the rhizosphere under the red versus white surfaces was less than 0.5°C. On 9 September shoots and roots were separated by cutting at the panel surfaces, roots were washed, and the shoots and roots were freeze-dried and weighed on a per plant basis. Shoot weight, root weight, and shoot/root biomass ratios were determined.

RESULTS AND DISCUSSION

Reflection from a Green Leaf Surface

A typical corn leaf reflected little of the R and much of the FR that impinged on its surface (Fig. 1). Notice that the FR reflection curve begins to plateau at about 750 nm.

If we extrapolate the FR reflection from a single green leaf to a field situation with variously spaced plants, the amount of reflected FR received by a growing plant should be influenced by the number, nearness, size, and orientation of competing leaves. Also, it was previously shown that heliotropic orientation of broad leaves with long petioles (such as soybean) can cause them to be directional FR reflectors (17, 20). The directional FR reflection from bean leaves has resulted in higher FR/R ratios in N-S rows relative to E-W rows, especially at low solar angles near the beginning and end of day [effects of FR/R ratio on photoequilibrium of the phytochrome system (13) at the end of day and effects on stem elongation and leaf shape (6, 9, 15) are well documented for plants grown in controlled environments]. Bean plants in N-S rows developed larger shoots (10, 20). While the spectral distribution of light reflected from individual corn leaves (see Fig. 1) was very similar to that reflected from individual soybean leaves (10), corn leaves do not track the sun. However, even a slight breeze can cause the corn leaves to flutter and thereby affect reflection patterns. These similarities in reflection spectra and differences in directional reflection between corn and bean leaves suggest that corn seedlings should be very responsive to nearness of other plants, but they should be less responsive to row orientation than was noted for beans.

Plant Spacing Effects on FR/R Ratio

Close-spaced 4-wk-old corn plants received more FR and higher FR/R ratios than wide-spaced plants on both the sun and the shade sides (Fig. 2). This is highly relevant in field-plant morphogenesis because growing plants respond to the FR/R ratio that exists during the photosynthetic period as well as at the end of day (18). It may be of biological significance that the FR reflection curve from the surface of a single leaf (see Fig. 1) and the amount of FR near close-spaced field plants (see Fig. 2) both begin to plateau at about 750 nm, well beyond the absorption peak (approximately 735 nm) of the FR-absorbing form of phytochrome. Earlier studies on the Beltsville Spectrograph (12) showed that plants display more pronounced stem elongation and leaf shape responses to prolonged irradiation at wavelengths of 750 to 760 nm than they do to prolonged irradiation at 735 nm. Another very relevant study was conducted by Vogelmann and Björn (25). They inserted fiber optic probes into fleshy leaves and found higher values at 750 nm within the tissue than at the exterior surface of the leaf. The increased values were attributed to light scattering and little competitive absorption at 750 nm within the tissue. On the other hand, the earlier studies on the spectrograph (12) also showed that the R-action peak for phytochrome regulation of morphogenesis in green plants is at about 645 nm because of competitive absorption by chlorophyll at 660 nm. Thus, a subtle shift in FR/R ratio at the exterior surface (5, 7, 12) of a plant could translate to a substantial shift in the photoequilibrium of the phytochrome system within the plant tissue (13, 21, 24, 25).

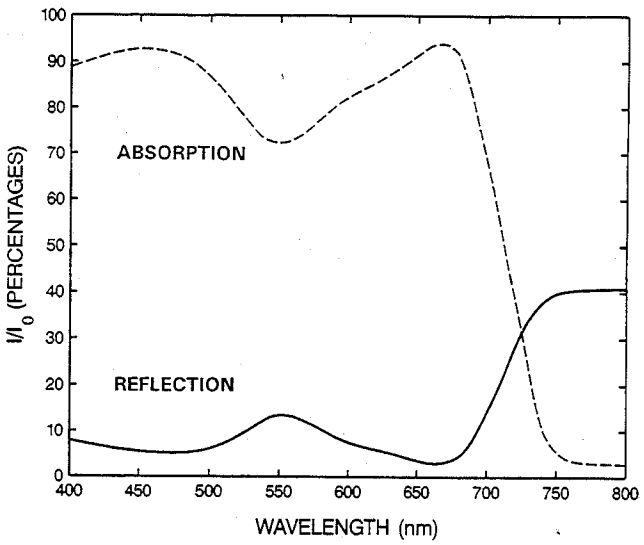

Fig. 1. Spectra of light absorbed by and reflected from the surface of an expanded corn leaf.

Row Orientation Effects on FR/R Ratios

The higher FR/R ratios received by close-spaced corn seedlings (see Fig. 2) were consistent with field grown soybean in which closer spaced plants also received higher FR/R ratios (10). However, unlike the soybean

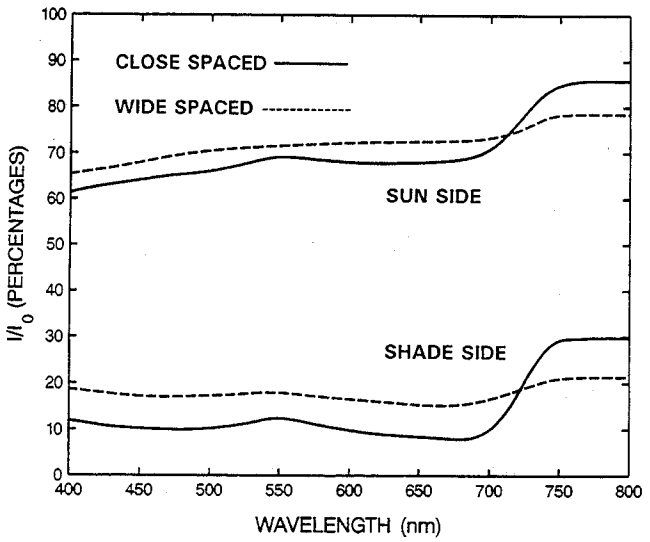

Fig. 2. Spectral distribution of light received on the sun side (top curves) and on the shade side (bottom curves) about 4.5 h before solar noon by upper (still expanding) leaves of 4-wk-old corn seedlings whose neighbors were 30 cm (solid line) or 120 cm (dashed line) away in field plots near Florence, SC. Similar curves for the sun and shade sides occurred about 4.5 h after solar noon.

row orientation effect on FR/R ratios (10), the FR/R ratios received by corn seedlings in N-S versus E-W rows did not differ significantly when plants were 25 cm apart in rows that were 75 cm apart in both directions in the present study (data not shown). Thus, nearness of competing plants resulted in the same general FR/R patterns for corn and soybean plants, but row orientation effects on the FR/R ratio were not evident for corn seedlings.

Morphogenic Responses to Nearness of Other Seedlings

Shoot Characteristics

Growth responses of corn seedlings to nearness of adjacent plants followed the same trends each year, and the year × spacing interactions did not differ significantly. Values in Table 1 are means for the 2 yr. Plants that received the highest FR/R ratio (the closest spaced ones) had the longest and narrowest leaf blades. They also had the thinnest leaves (milligrams of dry matter per square centimeter), the longest stems, the greatest stem dry weight, and the lowest leaf to stem dry weight ratio. Thus, the pattern of leaf/stem morphogenesis was significantly altered by the nearness of competing plants during the first weeks of growth, before mutual shading became a critical factor in photosynthesis.

Shoot/Root Relationships

The percentages of biomass allocated among shoots (leaves and stems) and roots of corn seedlings grown in the embedded cylinders differed among those grown in the three population densities. Shoot dry weights were largest and root dry weights smallest when the plants were grown in cylinders embedded in the 30- by 30-cm spatial arrangement. The shoot/root biomass ratios were 1.27, 1.03, and 0.83 for the closest, intermediate, and widest spacings, respectively. All of these plants had the same volume of the same soil mixture, but they were 30, 60, or 120 cm from the nearest corn plant in each direction. Since soil volume and root restriction did not differ among cylinders in the different populations, the differences in shoot/root biomass allocation are attributed to differences in FR/R ratio associated with nearness of other seedlings.

Table 1. Field plant spacing effects on leaf shape, stem length, and biomass distribution in shoots of 5-wk-old corn seedlings. Values are means for 2 yr.

	Plant spacing (cm)			LSD	
Characteristic	30 by 30	60 by 60	120 by 120	0.05	0.01
Largest leaf blade					
Length (mm)	799	756	708	22	30
Width (mm)	95	102	104	2	3
L/W (ratio)	8.42	7.39	6.80	0.23	0.31
All leaf blades					
Area (cm^2)	4048	4162	3594	215	288
mg dry wt/cm^2	4.72	5.26	5.48	0.20	0.27
Stem					
Length (mm)	342	254	180	24	32
Diam (mm)	23	27	28	0.9	1.2
Dry wt. (mg)	5263	4825	2972	657	879
Leaf†/stem (dry wt. ratio)	4.94	6.25	9.02	0.75	1.00

† Leaf weight includes blades plus sheaths.

It is apparent from these experiments that corn seedlings sensed the FR/R ratio in light as an indicator of competition from other plants, and that the ratio was involved in regulating physiological processes that resulted in prioritized allocation of photoassimilates in a manner that could favor survival among the perceived competition. For example, close-spaced seedlings received more reflected FR, which resulted in a higher FR/R ratio. The adaptive response was allocation of more photoassimilate to development of longer stems, and longer but narrower leaves (see Table 1). These shoot characteristics resulted in a greater probability of keeping some leaves in sunlight above the competing close-spaced plants, which could thereby increase probability of survival. While the close-spaced seedlings allocated more photoassimilate to stem growth, apparently less was left for root growth, as was observed when the cylinders were embedded within the different field plant spacings. Thus, corn seedlings like those of soybean (10) and cotton (16) were able to sense FR/R ratio long before mutual shading adversely affected the amount of photosynthetic light.

Morphogenic Responses to Row Orientation

Seedlings grown in N-S versus E-W rows did not differ significantly in leaf number, leaf area, leaf length, leaf width stem length, or leaf/stem biomass ratio (data not shown), when row spacing and within-row spacing were the same in both directions. This observation was consistent with the fact that FR/R ratios received by the seedlings in N-S versus E-W rows did not differ significantly with row orientation, as discussed above.

Morphogenic Responses to FR/R Ratio in Upwardly Reflected Light

Characteristics of upwardly reflected light above red and white soil-covered and painted insulation panels are shown in Table 2. Seedlings that were grown over both of the red surfaces received higher FR/R ratios in upwardly reflected light than those grown over the white surfaces. Within each surface material, plants over red developed larger shoots, less massive roots, and higher shoot/root biomass ratios. The response to spectra of upwardly reflected light from the two different surface coverings (soil and paint) as well as to spectra altered by reflection from nearby plants (see Table 1) suggests that morphology of corn seedlings can be influenced by FR/R ratio reflected from any nearby surface including natural soil, artificially colored surface covers (mulches), crop residues, or other nearby objects (including weed plants) that alter spectra of reflected light.

CONCLUSIONS

The leaf/stem and shoot/root photosynthate allocation patterns in response to FR/R ratio (which was influenced by FR reflected from nearby plants) in field-grown seed-

Table 2. Upwardly-reflected photosynthetic light and FR/R ratio 10 cm above white or red soil-covered or painted insulation panels, and shoot/root biomass distributions in corn seedlings grown over the panels from 14 August to 9 September in a greenhouse without supplemental lighting near Florence, SC.

	Panel surface and color			
	Soil		Paint	
Characteristic	Gray-white	Brick-red	White	Red
Upwardly reflected light† (relative to incoming sunlight)				
PPF (%)	36	13	44	16
FR/R (photon ratio)	1.00	1.18	1.00	1.11
Plant‡				
Shoot dry wt. (mg)	3759 ± 124	4232 ± 149	3561 ± 169	4121 ± 248
Root dry wt. (mg)	4249 ± 221	3512 ± 96	3608 ± 141	3168 ± 123
Shoot/root (wt. ratio)	0.88 ± 0.05	1.21 ± 0.04	0.99 ± 0.05	1.30 ± 0.08

† PPF, photosynthetic photon flux (400–700 nm); FR, far-red light (735 ± 5 nm); R, red light (645 ± 5 nm). FR/R ratio in incoming sunlight was assigned a value of 1.00.
‡ Values are means ± SE for eight plants. Ratios were calculated before rounding off.

lings was evident. The phytochrome system within the seedlings functioned as a sensor of competition (the FR/R ratio) and initiated physiological events that influenced prioritization in the allocation of new photoassimilates to the various components of the growing plant. For example, a seedling in the higher population density received more reflected FR and a higher FR/R ratio. The adaptive response was to allocate more of the new photosynthate for development of longer stems and longer leaves, both of which increased the probability that the plant would have some photosynthetic area above competing plants. When a greater fraction of new photosynthate was allocated to elongating stems, less remained for new root growth, and vice versa. Thus, the leaf/stem and shoot/root biomass ratios were altered in seedlings according to the FR/R ratio, which could be modified by FR reflection from other green plants or by the FR/R ratio in upwardly reflected light over different colored surfaces. We conclude that it is important to be aware of these adaptive morphological responses to light spectral consequences of plant spacing and soil surface color (including presence of any crop residues and mulches that might alter the FR/R ratio in reflected light), and to then use the information in development or modification of plant-soil-water-light management systems.

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