

SOYBEAN SPACING AND ROW ORIENTATION EFFECTS ON PHYTOCHROME REGULATION OF PLANT DEVELOPMENT

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ABSTRACT

Plant spacing and row orientation affected spectral distribution of light received by soybean [*Glycine max* (L.) Merr.] plants growing under field conditions. Light absorption, transmission and reflection of individual leaves showed that most of the blue and red was absorbed while most of the far-red was either transmitted or reflected. Plants received different ratios of far-red relative to red, depending on nearness and/or orientation of other plants. In close-spaced rows or high population densities, plants received higher far-red/red ratios than those grown in wide rows or sparse populations. Sun-tracking movements of the leaves contributed to the far-red reflection patterns associated with row orientation. 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 as a sensor of competition from other plants and a regulator of plant adaptation. Partitioning among plant components in the field was related to far-red/red light ratio received during growth and development.

INTRODUCTION

The process of photosynthesis and the partitioning of photoassimilates to developing seed is extremely important in soybean production. Many studies have emphasized canopy interception of photosynthetically active light, photosynthetic rates with different CO₂ levels and light intensities (fluence rates), and source-sink relationships in partitioning of photoassimilates within plants and especially to developing seeds. However, much less attention has been given to the effects of light environment during leaf development on the photosynthetic efficiency of those leaves, and on plant development. The purpose of the present report is to examine relationships among plant spacing, spectral distribution of light reflected from competing plants, far-red/red light ratios in canopy light, and phytochrome regulation of plant 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 over-seeded 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 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 far-red relative to red (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 chlorophyll competition for light at 660 nm (the phytochrome *in vitro* peak) shifts the phytochrome action peak to about 645 nm in green plants (Kasperbauer et al. 1963). Values for absorption by, transmission through, and reflection from single leaves were obtained using a LiCor-1800-12 integrating sphere.

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 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. All pots were watered with half-strength nutrient solution 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 days of cool-white fluorescent light at 520 $\mu\text{mol m}^{-2} \text{s}^{-1}$. 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 and FR radiation units were as used in earlier studies by Kasperbauer and Hamilton (1984). Daily R and FR treatments began when seedlings reached the unifoliolate leaf stage. Vegetative samples were taken after 20 days.

RESULTS AND DISCUSSION

Plants of the same genotype frequently differ in phenotypic development when grown in sparse relative to dense populations and to some extent when grown in north-south versus east-west rows. It is apparent that each plant is genetically programmed for a number of alternate developmental patterns and expression depends on the environmental combinations that exist during plant growth and development (Kasperbauer, 1988). Thus, it is important to realize that plants have evolved to survive in their environment long enough to produce its next generation, not necessarily to produce the highest yield for the grower. That is, the plant must be able to sense potential competition from other plants and to adapt developmental processes that favor its survival. For example, a plant surrounded by many other plants must develop a longer stem or be shaded out. This adaptation involves morphological development and regulation of photosynthate partitioning within the plant, including that to developing seeds. Awareness and management of natural regulation of plant development might lead to improved yield and/or quality of crop plants, including soybean.

In a recent study, Hunt et al. (1985) 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 plant growth and development, and higher from east-west rows when there was intermittent water stress, as

frequently occurs on the Southeastern Coastal Plain of the United States. It became apparent that row orientation in some way influenced plant shoot/root ratios which, in turn, may have influenced the plant response to intermittent water stress. A slightly larger shoot/root ratio might be advantageous if there was no water or nutrient stress, whereas it might be a disadvantage if sudden water stress occurred as it frequently does in non-irrigated fields of sandy soil. It is possible that: (1) there is some distinct environmental difference associated with differences in plant spacing and/or row orientation, (2) each plant contains a sensor of that environmental factor, and (3) the sensor within the plant is capable of initiating physiological changes that regulate partitioning of assimilates among developing leaves, stems, branches, roots, and seed within the plant. Perhaps some component of the light environment is involved.

Previous research on photo-regulation of plant morphogenesis under precisely controlled environments (Downs et al., 1957; Vince, 1964; Kasperbauer et al., 1963, 1964; Borthwick, 1972) suggested that spectral distribution of light might play a role in plant morphogenesis under field conditions. Even though early studies of light spectra under field conditions concentrated on light transmitted through leaves and into the canopy (Kasperbauer 1971; Holmes and Smith, 1977; Holmes 1981; Morgan, 1981), reflected light now appears to be a dominant factor in photomorphogenesis of crop plants under field conditions (Kasperbauer, 1987, 1988). Perhaps the best approach to this topic is to first consider what happens to the various wavelengths of light that reach the surface of a green leaf. Of course, the values differ somewhat with age of leaf, etc., but nearly all of the blue and red and most of the green wavelengths are absorbed. The absorption spectra from about 400 to just beyond 700 nm are consistent with the combined absorbencies of chlorophyll and the carotenoids, thus the term photosynthetically active radiation (PAR). Young green leaves absorb very little light beyond about 710 nm. Although PAR in plant canopies has been widely studied, plants also respond very dramatically to the 700 to 800 nm waveband, which we cannot see with the unaided eye. This waveband is referred to as far-red light (FR), and a better understanding of its presence and function should be useful in interpretation of plant morphological responses to spacing and row orientation.

Some key points to remember when studying plant development in different spatial arrangements are (1) the amount and nearness of other green plants influence the amount of reflected FR received by a growing plant, (2) other pigments within green leaves absorb most of the R and very little of the FR light, (3) the ratio of FR relative to R that reaches phytochrome within the plant tissue regulates photoequilibrium of the phytochrome system, and (4) the photoequilibrium level of the phytochrome system within the plant then initiates events that activate, or repress, genes that direct partitioning of photoassimilate among leaves, stems, branches, roots, and developing seed. A relationship between photoequilibrium level of phytochrome and the balance among various endogenous growth regulators is evident, but not understood. Basically, the individual plant senses competition from other plants and adapts in a manner to favor its own survival (Kasperbauer, 1988).

An example of the effects of nearness (row spacing) on the FR/R ratio and on plant development is shown in Table 1. There are several significant points: (1) the FR/R ratio in sunlight is lowest near noon and increases as the day progresses with values above 3.0 in the last few minutes before sunset (Kasperbauer, 1987), (2) plants in close-spaced rows receive higher FR/R ratios,

and (3) the highest ratios are found on the shaded side because of FR reflection back from the adjacent row.

Table 1. FR/R ratios in direct sunlight and at the surface of the upper canopy of 6-week-old soybean plants in 20- and 100-cm North-South rows near Florence, SC, August 1984 (Kasperbauer, 1987).

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

Table 2. Row orientation effects on shoot characteristics of 5-week-old soybean plants and on dry matter distribution in shoots of plants grown to ripeness in irrigated loamy sand field plots near Florence, SC. (Kasperbauer, 1987).

Row orientation	Plant characteristics						
	Per 5-week-old plant			Dry matter/m of row (20 plants)			
	Stem length	Leaves	Branches	Seed	Pods	Stems	Seed/straw
	(cm)	(no)	(no)	(g)	(g)	(g)	(ratio)
N-S	34.8	8.1	1.8	158.2	58.2	43.8	1.55
E-W	32.4	8.2	3.0	142.8	53.0	40.8	1.52
LSD 0.05	*	NS	*	*	NS	NS	-

Row orientation effects on the FR/R ratios were such that plants in north-south (N-S) rows received slightly higher ratios when averaged over the total day (Kasperbauer, 1987). The differences in FR/R ratio received at the canopy surface of plants in N-S versus E-W rows were greatest just before sunset. Presumably, heliotropic (sun-tracking) movement of the leaves was involved and resulted in directional reflection of FR. Plant characteristics of 5-week-old soybean seedlings in 80-cm rows are shown in Table 2. Plants in the N-S rows (which received slightly higher FR/R ratios) had longer stems and fewer branches than those in E-W rows. At time of harvest, the plants grown in N-S rows had higher seed yields, but the taller stems did not weigh significantly more than those from E-W rows. No leaf weights are shown because they had senesced and were not included in plant weights at harvest. It is of significance that seed yield of these soybean plants (which were grown on irrigated sandy soil of the South Carolina Coastal Plain) was consistent with the earlier results of Hunt et al., (1985). To test concepts of the involvement of reflected FR (via row orientation on plant growth) at another geographic location, an experiment was conducted at the Kentucky State University Research Farm near Frankfort in 1987 (Kaul and Kasperbauer, 1988). The experiment with bush bean (which has slightly larger leaves than soybean) showed a slightly higher row orientation effect on the amount of reflected FR, and plants in N-S rows developed larger shoots and

higher bean yields. Again, it should be noted that there was no water stress during the growing season.

Table 3. Percentages of dry matter partitioned among shoots and roots of soybean seedlings grown in a controlled environment with end-of-day treatment with R (low FR/R ratio), FR (high FR/R ratio) or FR followed immediately by R (high FR/R followed abruptly by low FR/R ratio) each day for 20 consecutive days (Kasperbauer, 1987).

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)

A number of other field experiments with various spatial configurations and row orientations supported the concept that the nearness, number, and orientation of competing leaves can influence the amount and pattern of reflected FR. This is important because the FR/R ratio in the field can influence the amount of shoot growth and the partitioning of photoassimilate among leaves, stems, branches, roots, and developing seed. These observations are consistent with a controlled environment study that utilized soybean plants inoculated with *B. japonicum* strain NC-1004 (Table 3). Clearly, the FR/R ratio of light at the end of each day, influenced partitioning of assimilate among plant components even though both R-treated and FR-treated plants received the same PAR (i.e. all received the same total light energy). The relative amounts partitioned to stem and root growth were very dramatic (Table 3), and the similarity of response to R alone and to R immediately following FR is evidence that the photoreversible pigment, phytochrome, is involved in measuring the amount of competition and in initiating physiological events that favor survival among the perceived competition. Examples of adaptive responses to higher FR/R ratios observed in previous studies include development of longer stems, less branching, and thinner leaves that have chloroplasts with more but smaller grana, a modified chlorophyll a/b ratio, higher concentrations of the light harvesting chlorophyll protein (LHC-II), and more CO₂-fixed per mass of leaf with a given amount of photosynthetic light (Kasperbauer, 1988; Bradblume, 1988).

CONCLUSIONS

Each plant is genetically programmed for alternate developmental patterns, and expression depends on growth environment. Plant spacing and row orientation can affect the FR/R ratio in reflected light. The FR/R ratio acts through the phytochrome system within a plant and regulates partitioning and use of photoassimilates. Variations as subtle as row orientation or relatively small differences in spacing can affect shoot/root ratio and seed yield per plant which might be important in water management especially on sandy soils with low water-holding capacity.

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