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Shoot/root assimilate allocation and nodulation of *Vigna unguiculata* seedlings as influenced by shoot light environment

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Abstract

Spectral balance of light received by southern pea [*Vigna unguiculata* (L.) Walp.] seedling shoots affected photoassimilate allocation among leaves, stems and roots. A higher ratio of far-red (FR) relative to red (R) light resulted in longer stems, higher shoot/root biomass ratio, less massive roots and fewer nodules. The same response pattern to FR/R ratio was obtained in a controlled environment with artificial light sources, or in sunlight where the FR/R ratio was modified by reflection from different colored soil surfaces or by FR reflected from competing plants. The importance of early shoot/root photoassimilate allocation and nodulation may differ according to soil nitrogen availability and moisture content.

Introduction

Early nodulation and N_2 fixation are important in legume crops, especially when grown on N-deficient soils. Allocation of photoassimilates to roots is essential for nodule formation, and light environment of the shoot can influence allocation among growing plant parts. Downs et al. (1957) showed that brief exposures to red (R) or far-red (FR) light at the end of the day could influence stem length. Hendricks and Borthwick (1967) attributed regulation of seedling shoot morphogenesis to the action of phytochrome. Kasperbauer et al. (1964) noted that seedling shoots were morphologically responsive to prolonged exposures to FR wavelengths beyond the absorption peak for the FR-absorbing form of phytochrome. Kasperbauer (1971) used hydroponic grown seedlings to demonstrate the effect of FR/R ratio on biomass allocation among leaves, stems and roots. That work was extended to controlled-environment grown soybean [*Glycine max* (L.) Merr.] seedlings to demonstrate that the FR/R ratio at the end of the photosynthetic period could affect nodulation as well as shoot/root ratios (Kasperbauer et al., 1984). Greater photoassimilate allocation to roots was associated with formation of more nodules, and the affect of FR/R ratio on nodulation was greater on seedlings grown in potting medium with low available-N content. The research reported in this paper was conducted to determine whether spectral balance of light received by southern pea seedling shoots could affect photoassimilate allocation and nodulation during early seedling growth in sunlight.

Materials and methods

Southern pea [*Vigna unguiculata* (L.) Walp. cv. Mississippi Silver] seedlings were grown in individual containers in each of the three experiments so that roots as well as shoots could be evaluated after the treatment periods. At the end of each

experiment, stems were measured, roots were washed, nodules were counted, and plants were separated into component parts. The parts were freeze-dried and weighed. Data are presented as means per plant ± S.E.

Controlled environment.

Seedlings were started and grown in 3-L pots of a 1:1 mixture of potting soil (Pro-Mix-BX, Premier Brands Inc., Red Hill, PA) and vermiculite. The seeds were inoculated with the S strain of *Bradyrhizobium japonicum* (Nitragin Co., Milwaukee, WI). All seedlings were grown in the same controlled environment chambers where they received 12 h photosynthetic periods from cool-white fluorescent lamps at 520 μmol m^{-2} s^{-1} and day/night temperatures of 27±2°C. At the end of the daily photosynthetic period, plants were exposed to either 5 min of R (3.6 Wm^{-2} in the 600–700 nm waveband), 5 min FR (3.6 Wm^{-2} in the 700–770 waveband), or 5 min FR followed immediately by 5 min R. The R and FR radiation units were as described by Kasperbauer (1987). Plants remained in uninterrupted darkness for 12 h after the R or FR treatments. Thus, the seedlings received the same treatment except for R and FR at the end of each day to put phytochrome predominantly in the FR-absorbing or the R-absorbing form, respectively, at the beginning of each night. The R and FR treatments began when the seedlings were in the unifoliate stage, and the same procedure was followed each day for 28 days until plants were evaluated.

Soil surface color effects.

Seeds were sown in 3-L pots of Norfolk loamy sand and placed 60 cm apart in groups of four on greenhouse benches. The loamy sand was taken from field plots previously used for southern pea. The soil 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 × 122 × 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 insulation panels were covered with about 1 cm of white or brick-red soil. Spectral distributions of light reflected from the soils were measured 10 cm above these surfaces. Spectral measurements were taken at 5 nm intervals from 400 to 800 nm with a LiCor-1800 Spectroradiometer (LiCor, Lincoln, NE.) equipped with a remote, hemispherical, cosine-corrected light collector on a 1.5 m fiber optic probe. Incoming sunlight was measured and the reflected light values were then calculated as percentages of the incoming sunlight at each measured wavelength. 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 chlorophyll competition for light at 660 nm (the approximate phytochrome absorbance maximum in vitro) shifts the action peak to about 645 nm in green plants (Kasperbauer et al., 1964). The FR/R ratios shown in this report are relative to the ratio in direct sunlight, which was arbitrarily assigned a value of 1.00. The rationale for this approach is that plants are adapted to sunlight, and a FR/R ratio that deviates from that in direct sunlight might signal the plant to activate or repress genes that regulate adaptation to the altered light environment (Kasperbauer, 1988). The reflected light measurements were taken at solar noon ± 30 min on a clear day. Soil temperatures below the white and red surfaced 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 difference in the pots (root zone) below the insulation panels with the two different soil colors was less than 0.5°C. This approach allowed comparison of seedling morphological development over different colored soils when effects of soil surface color on rhizosphere temperature were minimized below the soil colors. There were eight plants per soil color. Seedlings were evaluated after 18 days.

Row orientation effects

Seeds were sown in 10 cm (diam.) × 45 cm polyvinyl chloride cylinders of Norfolk loamy sand that were embedded in field plots in north-south (N-S) versus east-west (E-W) rows that were 50 cm apart. This procedure was used in order to recover roots and nodules from seedlings grown in NS and EW rows. There were eight rows in each direction. Two cylinders were embedded in each of four rows in each direction. At emergence, seedlings were thinned to 5 cm apart within rows. Only one seedling was kept per cylinder. The plant spacing in rows between and within the cylinders provided similar amounts of leaf surface to reflect FR. Light measurements were recorded at about 1700 h on a cloudless day to determine row orientation effects on heliotropic influenced directional reflection of FR and on FR/R ratios received by seedlings that were growing in the cylinders. Seedlings were removed from the cylinders and evaluated after 30 days.

Results and discussion

Photoreversible effects of R and FR on assimilate allocation.

When photosynthetic light was held constant in a controlled environment, southern pea seedlings responded morphologically to R or FR received for 5 min at the end of the photosynthetic period (Table 1). The fact that plants responded to brief exposures to R (low FR/R ratio) and FR (high FR/R ratio) and that the effects of FR were reversed by R is consistent with the hypothesis that phytochrome functions in an environment-sensing mechanism that regulates photosynthate allocation among developing plant parts. In addition to having longer internodes, seedlings that received FR last each day (high FR/R ratio) developed less massive roots and a higher shoot/root biomass ratio. Seedlings whose shoots received the high FR/R ratio developed fewer nodules during the treatment period. Results of the controlled-environment study suggest that field management systems which modify the FR/R ratio received by growing southern pea seedlings should also result in modified photosynthate allocation and the amount of nodulation. To test this theory, southern pea seedlings were grown in soil with low available-N; and the FR/R ratio reaching the seedlings was modified by growing them over soil surfaces that reflected different FR/R ratios, and by growing seedlings in N-S versus E-W rows which differed in FR/R ratio because heliotropic leaf movement caused them to be directional FR reflectors (see Kasperbauer, 1987) near the end of each day.

Soil surface color effects.

Seedlings grown in sunlight over the soil surface color that reflected the higher FR/R ratio developed longer stems, a higher shoot/root biomass ratio, less massive roots, and fewer nodules (Table 2). The phytochrome system within the young seedlings apparently sensed the FR/R ratio reflected from the soil surface and initiated physiological processes that resulted in allocation of photoassimilate among growing plant parts, just as would occur if the FR/R ratio was altered in a controlled environment (Table 1) or by FR reflected from leaves of competing plants, as discussed below. Under field conditions the FR/R ratio reflected from the soil surface could also be influenced by plant residues from previous crops in conservation tillage systems, low growing weeds, or artificially colored mulches (Hunt et al., 1989; Kasperbauer and Hunt, 1987, 1992).

Row orientation effects.

In field plots, row orientation influenced the amount of reflected FR and the FR/R ratio received by nearby seedlings (Table 3). Green leaves absorbed most of the incoming R, but they reflected or transmitted most of the FR. Because of heliotropic (sun tracking) movement of southern pea leaves, they became directional FR reflectors. Seedlings in N-S rows received more reflected FR and higher FR/R ratios near the end of each day. The patterns were very similar to those pre-

Table 1. Shoot and root size and nodulation of southern pea seedlings in a controlled environment with 5 min end-of-day treatment with red (R, low FR/R ratio), far-red (FR, high FR/R ratio), or FR followed immediately by R each day for 28 consecutive days

Character	End-of-day-light		
	R	FR	FR,R
Stem length (mm)	164 ± 7[a]	277 ± 13	155 ± 8
Shoot/root (dry wt. ratio)	3.03 ± .27	4.01 ± .43	3.34 ± .20
Root dry wt. (mg)	997 ± 179	645 ± 71	906 ± 91
Nodules (no)	29 ± 10	8 ± 4	36 ± 13

[a] Values are means for 10 plants ± S.E.

Table 2. Shoot and root size and nodulation of southern pea seedlings grown on a greenhouse bench in sunlight for 18 days over different colored soils covering insulation panels

	Soil color	
	Gray-white	Brick-red
Upwardly reflected light (relative to incoming sunlight)[a]		
PAR(%)	24	10
FR/R (ratio)	1.00	1.18
Plant[b]		
Stem length (mm)	145 ± 3	156 ± 7
Shoot/root (dry wt. ratio)	2.47 ± .16	2.88 ± .13
Root dry wt. (mg)	1753 ± 157	1374 ± 119
Nodule dry wt. (mg)	93 ± 19	45 ± 14
Nodules (no)	176 ± 26	108 ± 29

[a] PAR, photosynthetically active radiation; FR/R, photon ratio at 735 nm relative to 645 nm. The FR/R ratios in upwardly reflected light are expressed relative to ratio in incoming sunlight, which was assigned a value of 1.00.
[b] Values are means for eight plants ± S.E.

viously reported for *Phaseolus vulgaris* L. (Kaul and Kasperbauer, 1988). Southern pea seedlings grown in cylinders that were embedded in the N-S rows developed longer stems, higher shoot/root biomass ratios, less massive roots, and fewer nodules (Table 3).

It is evident that the phytochrome system within the seedlings responded to the FR/R ratio as a "signal" of potential competition from other plants (FR reflectors). The adaptive response to a higher FR/R ratio was to allocate more photosynthate to developing stems, leaving less for new root growth. Less photoassimilate allocation to roots also resulted in less nodulation. In nature, the adaptive advantage of longer stems is that they increase the probability of plant survival because some leaves would be in photosynthetic sunlight above competing plants. Awareness of natural bioregulatory systems should be useful in developing field crop management systems. The importance of early shoot/root photoassimilate allocation and nodulation may differ

Table 3. Shoot and root size and nodulation of southern pea seedlings grown in field plots for 30 days in cylinders of loamy sand embedded in east-west (E-W) versus north-south (N-S) rows that were 50 cm apart

Character	Row orientation	
	E-W	N-S
Light[a]		
FR/R (ratio)	1.05	1.15
Plant[b]		
Stem length (mm)	140 ± 8	175 ± 6
Shoot/root (dry wt. ratio)	2.60 ± 0.23	3.06 ± 0.29
Root dry wt. (mg)	902 ± 81	806 ± 74
Nodule dry wt. (mg)	35 ± 9	19 ± 6
Nodules (no)	78 ± 10	55 ± 8

[a] FR/R, photon ratio at 735 nm relative to 645 nm. Spectra of light coming to shoot tips were measured parallel to the ground from N, S, E and W at 1700 h on a cloudless day, and the ratios are means for 8 measurements (2 each from N,S, E and W).
[b] Values are means for eight plants ± S.E.

according to soil N availability and soil moisture content. We hypothesize that E-W row orientation of southern pea and other legume seedlings on low-N, droughty soils might have the advantage of more massive roots, less moisture stress, more early nodulation and N_2 fixation, and greater productivity; whereas N-S row orientation could favor greater shoot growth and increased productivity on soils with high available-N and no water stress.

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