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Light-mediated bioregulation of tillering and photosynthate partitioning in wheat

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The influence of plant population density on spectral distribution of light received by wheat (*Triticum aestivum* L. cv. Coker 797) seedlings was measured under field conditions, and effects of red and far-red light on tillering and photosynthate partitioning were studied in controlled environments. Spectral distribution of light was measured in sunflecks at soil level in close-, intermediate-, and wide-spaced field populations during the tillering stage. Close-spaced seedlings received higher far-red/red light ratios than wide-spaced plants because of the larger amount of far-red reflected from green leaves of the more numerous nearby plants. The far-red/red light ratios in all population densities were higher in late afternoon than at noon. Close-spaced plants developed fewer tillers, less roots and longer leaves than wide-spaced seedlings under field conditions. In controlled environments, a higher far-red/red ratio during photosynthetic periods resulted in fewer tillers and longer leaves; whereas, brief red or far-red exposures at the end of each day had a more pronounced effect. Wheat seedlings that received 5-min exposures to far-red light at the end of the photosynthetic period each day for 20 consecutive days developed fewer tillers, longer leaves, less roots, and a higher shoot/root biomass ratio. The effects of far-red light were reversed by red light. The light spectral shifts associated with field plant population densities and the responses to red and far-red treatments under controlled environments suggest that phytochrome serves as a sensing mechanism that detects the amount of competition from other plants, and regulates the development of tillers and the partitioning of photosynthate between shoots and roots.

Additional key words – Phytochrome, shoot/root ratios, *Triticum aestivum*.

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Introduction

Better understanding of natural bioregulation of plant physiological processes is important in developing a total plant-soil-water management system. For example, wheat (*Triticum aestivum* L.) seedlings develop various numbers of tillers depending on growth conditions, and the tillers are important because they increase the photosynthetic area and produce additional seed per plant. The number of tillers per plant is generally low when plants are crowded and much higher when wide apart. Apparently, each individual plant can sense the closeness of competing plants and is able to adjust its physiological processes, including the formation of tillers.

The influence of light spectral distribution upon branching of dicotyledons has been demonstrated for tomato (*Lycopersicon esculentum* Mill.) seedlings (Tucker 1975), pea (*Pisum sativum* L.) seedlings (Khudairi et al. 1971), tobacco (*Nicotiana tabacum* L.) (Kasperbauer 1971) and young soybean [*Glycine max* (L.) Merr.] plants (Kasperbauer et al. 1984). Far-red-enriched light generally results in suppressed branching of dicots. Spectral shifts within plant canopies, and effects on form of phytochrome in plants have been studied by

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several investigators (Holmes 1981, Holmes and Smith 1977, Kasperbauer 1971, Schäfer 1981, Smith and Holmes 1977).

Some management practices such as grazing or partial defoliation result in increased tillering of grasses (Youngner 1972). However, relationships among field plant density, spectral distribution of light and tillering have not been reported. The objectives of the present study were to (a) measure spectral distribution of light in various field populations of wheat during the tillering stage and (b) measure effects of R and FR during the photosynthetic period as well as at the end of the photosynthetic period on tillering and photosynthate partitioning among plant components.

Abbreviations – FR, far-red light; P_r, red-absorbing form of phytochrome; P_{fr}, far-red-absorbing form of phytochrome; R, red light.

Materials and methods

Field

Plants. Wheat (*Triticum aestivum* L. cv. Coker 797) was sown in November 1983 on a Norfolk sandy loam (Typic Paleudults) in the Southeastern Coastal Plain near Florence, SC. The densities of seedling populations were ca. 30 m^{-2} (wide), 120 m^{-2} (intermediate), and 300 m^{-2} (close). Plots were fertilized according to Clemson Agricultural Experiment Station recommendations (Anon. 1982) and irrigated as needed.

Light measurements. Spectral distributions of light were measured at 5-nm intervals from 350 to 850 nm in the plant canopies with a LiCor Spectroradiometer Model 1800 with a remote cosine collector on a 1.5-m fiber optic probe. The collector target was less than 1 cm in diameter, which allowed measurements in small sunflecks as well as in shade. Light measurements were taken at soil level when plants were in the tillering stage [Stage 6 of the Feekes scale for growth and development of wheat (Large 1954)] to determine spectral differences associated with plant population densities, and a possible relationship between spectral balance of light and tiller development. The effects of plant population on spectral distribution of light were assessed relative to direct sunlight. Reference spectra from 350 to 850 nm were taken at 5-nm intervals in direct sunlight 2 m above the soil surface. Spectral shifts within the wheat canopies were determined relative to reference spectra of direct sunlight taken within a few minutes of the respective canopy scans.

Spectral irradiances at 735 nm and 645 nm were used to calculate the FR/R ratios. These values were used because they correspond to phytochrome action peaks in green plants (Kasperbauer et al. 1963).

Tillers and partitioning. Tillers per plant were counted during the tillering stage and again after the plants had matured. Parameters determined in the mature plants were tillers per plant, spikes per plant, seed per spike and weight per 1000 seed. Straw biomass per plant and seed/straw biomass ratios were also determined.

Controlled environments

Wheat seedlings (cv. Coker 797) were started and grown in 3.5-l pots in a 1:1 (v/v) mixture of greenhouse potting soil (Pro-mix BX) and vermiculite. Pots were 18-cm in diameter. All seedlings were grown for the first 14 days at 20°C under 12-h days from cool-white fluorescent lamps. Pots were overseeded and thinned to six per pot for the light treatments.

FR/R ratios during photosynthetic period. Plants were grown under two different FR/R ratios during the daily photosynthetic periods. Two separate growth chambers were used. Both were Percival Model PGW-108 with plexiglas light diffusers below the lamps. Chamber I had 28 Sylvania VHO cool-white fluorescent lamps, and Chamber II had 28 Sylvania VHO cool-white fluorescent lamps plus 12 standard 100-W white incandescent-filament lamps to obtain different FR/R ratios during the photosynthetic periods. Bench elevations were adjusted to give 520 μmol m^{-2} s^{-1} of photosynthetically-active radiation at plant level in each chamber. Spectral distributions of light in the two chambers are shown in Fig. 1. The FR/R ratio during the photosynthetic period was about 5.0 times higher in Chamber II than in Chamber I. Photosynthetic periods were 12-h per day at 20°C. The fluorescent and incandescent-filament lamps in Chamber II were controlled by the same on/off switch.

FR/R at end of photosynthetic period. Some of the plants grown in Chambers I and II, as described above, received brief irradiations with R or FR (Kasperbauer and Hamilton 1984) at the end of the daily 12-h photosynthetic period. Plants received 5 min of R (3.6 W m^{-2} in the 600 to 700 nm waveband) or 5 min of FR (3.6 W m^{-2} in the 700 to 770 nm waveband) and then returned to darkness in the respective growth chamber for the remainder of the 12-h night. A third set received 5 min FR followed immediately by 5 min of R. Another group in each chamber received neither R nor FR at the end of the photosynthetic period. The R and FR treatments began 14 days after seeds were sown. There were five pots per light treatment from each of the two chambers. The R and FR treatments were repeated each day for 20 days. At the end of the 12-h dark period following the last R and FR treatments, tillers were counted and leaf lengths were measured on all plants. The plants were divided into shoots and roots, freeze-dried and weighed to obtain dry weights.

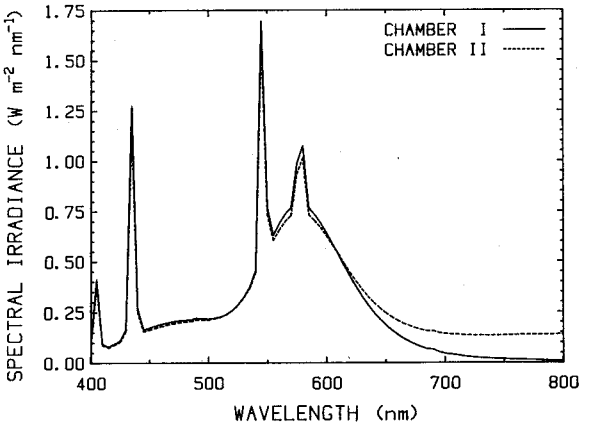

Fig. 1. Spectral distribution of light in Chamber I (solid line) and Chamber II (dashed line).

Results and discussion

Field

Spectral distribution of light in sunflecks and shade of wheat canopies during the tillering stage are shown in Fig. 2. Measurements were taken at soil level because tillers are initiated near the soil surface, and light environment might influence the amount of tillering in wheat, as it does branching in dicotyledons. Spectral shifts (Fig. 2) and FR relative to R ratios (Tab. 1) in sunflecks were greatest in close-spaced plant populations. The FR/R ratios increased due to solar angle as the day progressed, being greater near the end of the day than near noon. Also, the differences in FR/R ratios among plant population densities were much greater near the end of the day than near mid-day. It was apparent that

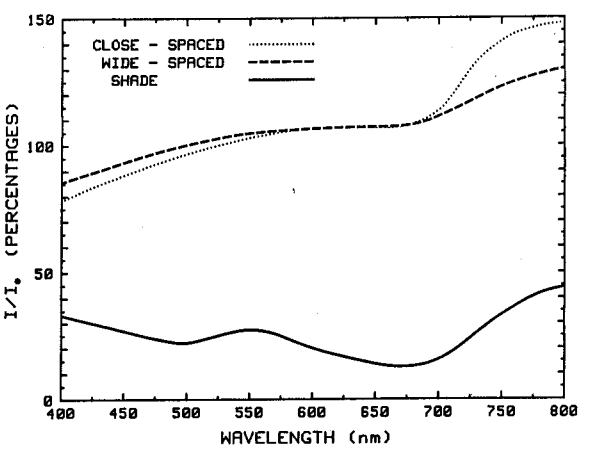

Fig. 2. Spectral distribution of light in sunflecks (dashed lines) and shade (solid lines) at soil level in early afternoon March 14, 1984, near Florence, SC. Values are expressed as percentages of direct sunlight measured 2 m above the canopy.

Tab. 1. Ratios of far-red relative to red light in direct sunlight 2 m above the soil and in sunflecks at soil level in three wheat population densities at tillering stage on a clear day near Florence, SC on March 14, 1984.

Time h	Direct sunlight	Plant spacing		
		Wide	Intermediate	Close
13 00	0.86	0.93	0.96	0.98
17 20	0.91	1.15	1.44	1.72

the higher amounts of FR relative to R among the close-spaced plants was related to greater amounts of FR being reflected from the more numerous green leaves. Plants from the close spacing developed fewer tillers and had longer leaves than those from the wide spacing (Fig. 3). The close-spaced plants had an average of 2.9 tillers while the wide-spaced ones had an average of 14.0 tillers at the stage shown in Fig. 3. The greater tiller numbers that developed on the wide-spaced plants tended to diminish the differences in spectral distributions among populations as the plants developed (M. J. Kasperbauer and W. Sanders, unpublished data). These observations suggest that natural bioregulation of tiller-

Fig. 3. Representative plants from wide- (L) and close-spaced (R) wheat populations.

Tab. 2. Characteristics of mature wheat plants grown in three field population densities.

Plant characteristic	Plant spacing		
	Wide	Intermediate	Close
Tillers/plant	10.2±0.7	3.6±0.2	1.9±0.1
Spikes/plant	9.8±0.6	3.5±0.2	1.8±0.1
Seed/plant	331±36	102±6	45±3
Seed/spike	33.5±2.0	29.2±0.8	24.8±1.0
DW (g)/1000 seed	33.1±1.0	33.2±0.6	29.5±0.6
Seed DW (g)/plant	11.0±1.1	3.4±0.2	1.3±0.1
Straw DW (g)/plant	14.5±1.8	5.0±0.2	2.1±0.2
Seed/straw biomass ratio	0.76	0.68	0.62

ing (branching) in wheat is controlled by the relative amounts of FR and R acting through a sensing mechanism which signals the plant how to adapt to improve its chances for survival and for seed production under the sensed growth environment.

The number of tillers per plant, spikes per plant and the seed and straw biomasses (Tab. 2) in mature plants from the three population densities support the above hypothesis. Plants from the least crowded populations had more tillers, more seed and a higher seed to straw ratio. We further hypothesized that differences in morphological development among the various plant spacings were related to different FR to R ratios that resulted from the absorption of R by chlorophyll and transmission or reflection of FR from green leaves. Thus, a plant in a higher population density would receive relatively more FR because of the reflection of FR light from more numerous nearby leaves. This would account for a lower photoequilibrium ratio of P_{fr} relative to P_r in the crowded plants which, in turn, would direct physiological events that regulate amount of tillering and partitioning of photosynthate. This could lead to physiological adaptation for better plant survival in the perceived environment.

Controlled environments

The FR/R ratios during the photosynthetic period and also at the end of the photosynthetic period influenced tillering and photosynthate partitioning of wheat (Tabs 3 and 4). Lower FR/R ratios during the photosynthetic periods (cool-white fluorescent) resulted in slightly more tillers and shorter leaves. Also, the R and FR treatments at the end of the daily photosynthetic periods significantly influenced the amount of tillering and the relative amounts of photosynthate partitioned among shoots and roots (Tab. 4). Reversibility of the effects of FR by the brief exposure to R supports the concept that phytochrome is the sensing mechanism.

The controlled-environment experiments supported the hypothesis that the amounts of FR relative to R received during wheat seedling growth can regulate the

Tab. 3. Effects of spectral balance of light during the photosynthetic period on tillering and photosynthate partitioning between shoots and roots in controlled environments. C-W Fl, cool-white fluorescent; C-W Fl + Inc, cool-white fluorescent plus incandescent.

Photosynthetic light	Tillers per plant (no.)	Leaf length (mm)	Shoot/root biomass (ratio)
C-W Fl	7.5±0.14	436±2.7	1.23
C-W Fl + Inc.	7.1±0.12	440±2.3	1.28

amount of tillering and the partitioning of photosynthate among shoots and roots. Pot cultures were used in the controlled environments to minimize effects of nutrients, water, temperature, photoperiod and total light energy. Thus, the observed plant characteristics can be attributed to differences in light spectra acting through a sensing system (phytochrome) within each individual plant. Phytochrome regulated the physiological processes leading to characteristics such as tillering, plant height and shoot/root biomass ratios.

These observations suggest that cultural practices which result in altered FR/R ratios, especially near the end of the daily photosynthetic period, can alter tillering and the shoot to root ratios of wheat seedlings under field conditions. This might be important for wheat plant survival and productivity on soils with low water-holding capacity or intermittent low water availability.

We recently showed that row orientation influenced the FR/R ratio of light received by soybean seedlings (Kasperbauer et al. 1984). Those in north-south rows received higher FR/R ratios. Also, R and FR acting through the phytochrome system regulated photosynthate partitioning among soybean shoots and roots under controlled environments. Plants that received relatively more FR partitioned more photosynthate to

Tab. 4. Effects of phytochrome on tillering of wheat and on partitioning between shoots and roots in controlled environments. Red (R) and far-red (FR) treatments were for 5 min at the end of the photosynthetic period each day for 20 consecutive days. Observations were recorded at the end of the 20-day treatment period.

Photosynthetic light	End-of-day light	Tillers per plant (no.)	Leaf length (mm)	Shoot/root biomass (ratio)
Cool-white fluorescent				
	R	8.7±0.3	425±5	1.09
	FR	5.4±0.3	460±5	1.36
	FR + R	8.1±0.2	420±5	1.10
Cool-white fluorescent plus white incandescent				
	R	7.9±0.2	429±5	1.24
	FR	5.9±0.3	453±6	1.42
	FR + R	7.8±0.2	436±5	1.14

shoots and less to roots. This was consistent with field observations (Hunt et al. 1985) which showed that soybean seed yields on sandy soil with low water-holding capacity were generally higher in north-south rows when water was not limiting (irrigated) and higher in east-west rows when occasional water stress occurred (non-irrigated).

Since tillering and the shoot to root ratios of wheat seedlings can be bioregulated by the relative amount of R and FR (Tabs 1–4), it is possible that management practices as subtle as direction of the drill rows might influence light spectral distribution sufficiently to affect plant survival, and perhaps yields under marginal soil moisture conditions. This potential application of light-mediated bioregulation is under further investigation.

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