Morphological Responses of Wheat to Blue Light

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Summary

Blue light significantly increased tillering in wheat (*Triticum aestivum* L.) plants grown at the same photosynthetic photon flux (PPF). Plants were grown under two levels of blue light (400–500 nm) in a controlled environment with continuous irradiation. Plants received either 50 μmol m⁻² s⁻¹ of blue light or 2 μmol m⁻² s⁻¹ blue light from filtered metal halide lamps at a total irradiance of 200 μmol m⁻² s⁻¹ PPF (400–700 nm). Plants tillered an average of 25% more under the higher level of blue light. Blue light also caused a small, but consistent, increase in main culm development, measured as Haun stage. Leaf length was reduced by higher levels of blue light, while plant dry-mass was not significantly affected by blue light. Applying the principle of equivalent light action, the results suggest that tillering and leaf elongation are mediated by the blue-UV light receptor(s) because phytochrome photoequilibrium for each treatment were nearly identical.

Key words: Blue light, phytochrome photoequilibrium, tillering, Haun stage, *Triticum aestivum*.

Abbreviations: PPF = photosynthetic photon flux; CELSS = controlled ecological life support system; PAR = photosynthetical active radiation.

Introduction

The morphology of grasses is affected by radiation quantity and quality. Radiation quality, measured as the spectral energy distribution (SED), has been shown to alter tillering in wheat and other grasses via effects on phytochrome photoequilibrium (Barnes and Bugbee, 1991; Kasperbauer and Karlan, 1986), but the effects of blue light, mediated by the blue light photoreceptor(s), have not been widely studied.

Inhibition of stem extension in dicots by short-term exposure (minutes or hours) to blue light has been demonstrated by many researchers (Casal and Smith, 1989; Cosgrove, 1981; Gaba et al., 1984; Warpeha and Kaufman, 1989, 1990).

Few studies, however, have examined long-term effects (days or weeks) of blue light on plants. Wheeler et al. (1991) reported blue light induced reductions in stem elongation of soybeans grown for 28 d under high-pressure sodium lamps. Increased amounts of blue light at constant PPF decreased stem elongation up to maximum of 50% with 35 μmol m⁻² s⁻¹ of supplemental blue light, suggesting that suppression of stem extension by blue light in soybeans is saturated at this level.

The exact mechanisms of blue light detection and subsequent plant response are not yet known. Rather than a single photo-sensing molecule, as in the case of phytochrome, the blue-UV light detecting mechanism in plants may be a group of photoreceptors, none of which has yet been identified; thus the nickname, cryptochrome (Senger, 1984). It is thought that cryptochrome may act in concert with other photoreceptors, especially phytochrome, perhaps enabling them to express their final action in plant responses (Mohr, 1986). The possible interactions between these photosystems must be considered when interpreting results.

The examination of spectral effects on plant growth is an important part of NASA’s effort to develop a Controlled...
Ecological Life Support System (CELSS), which may be an integral part of off-world human colonies (Bredt, 1988; Olson et al., 1988). Wheat (Triticum aestivum L.) cultivars grown under low-stress conditions typical of those in a CELSS produce more tillers than the same wheat cultivars grown in the field (Salisbury and Bugbee, 1988). Wheat crops that produce fewer tillers may be more productive in a controlled environment than those that tiller profusely because: 1) a crop composed of single-headed plants can be harvested earlier since the primary head of each plant matures first and, 2) primary heads have a higher harvest index — the ratio of edible to total biomass (Bugbee and Salisbury, 1988). Thus, reducing or eliminating tillering in controlled environments might increase yield, especially yield-per-unit time. Recent studies in our laboratory indicate that tillering can be reduced by altering radiation to simulate the phytochrome photoequilibrium that occur in deep shade (Barnes and Bugbee, 1991). This study sought to determine the effect of blue (400–500 nm) light on tillering in wheat when the phytochrome photoequilibrium was held constant. In addition, because plant height is of concern in controlled environments (volume may be a limiting factor in a CELSS) and because blue light is known to inhibit stem elongation (Cosgrove, 1981; Gaba et al., 1984; Warpels and Kaufman, 1990), we also investigated the effect of blue light on leaf and sheath elongation.

Materials and Methods

Cultural Procedures

Wheat (Triticum aestivum L. cv. Fielder) seeds were sown into soilless media (equal parts peat moss, perlite and vermiculite) in plastic pots (120 x 120 x 100 mm) and germinated at 23 °C in two sections of a six-sectioned, illuminated growth chamber (in which other experiments were simultaneously conducted). Each treatment section contained 24 (trial 1) or 20 (trials 2–3) pots. Plants emerged uniformly in both treatments after 3 d and were thinned to one plant per pot 5 d after planting. All plants were then of approximately equal size and were rotated within each treatment every 3 to 4 d to maintain uniformity. All sections were connected to a common air conditioning system, so CO₂, humidity, and temperature were nearly identical. Pots in both treatments were watered daily with approximately 300 mL of a dilute fertilizer solution (Peter's 20-5-30 NPK at 100 mg L⁻¹ nitrogen). Temperature was maintained at 21.5 ± 0.5 °C in both sections throughout the trial. The atmosphere was enriched with CO₂ to approximately 1000 μmol mol⁻¹ to increase the rate of carbon assimilation.

Spectral Treatments

Control plants were exposed to white light (high) blue treatment from a 1000-W metal halide (MH) lamp (Sylvania) passing through a 5-cm water bath and 9-mm plexiglass barrier (Dupont Lucite acryl). Plants in the reduced (low) blue treatment were exposed to radiation additionally filtered through a yellow (Rosco R161 «Canary Yellow») filter that removed approximately 96% of the blue photons.

Radiation Measurements

Relative contribution of blue (400–500 nm) photons to total photosynthetically active radiation (PAR) in each treatment was determined with a computer-driven spectroradiometer (Hewlett-Packard model HP-85 computer and an Optronics model 740-A spectroradiometer). Photosynthetic photon flux (PPF) was routinely measured with a quantum sensor (Li-Cor model LI-188B) and corroborated with the same spectroradiometer. Control plants (high blue treatment) received 200 μmol m⁻² s⁻¹ of continuous PPF, of which 50 μmol m⁻² s⁻¹ were blue photons. Plants in the low blue treatment also received a continuous 200 μmol m⁻² s⁻¹ PPF, of which 2 μmol m⁻² s⁻¹ were blue photons.

Phytochrome photoequilibrium, the fraction of total phytochrome in the active state (Pr/Prtot, or ϕ), was determined for each treatment from the spectroradiometric data using the method of Sager et al. (1988). Values for ϕ were 0.81 for the high blue treatment and 0.83 for the low blue treatment.

Plant Measurements

At each harvest, tiller number, main culm development, dry weight, and the length of the longest fully extended leaf were determined. Main culm development was measured as Haun stage (Haun, 1973), using the method of Klepper et al. (1985). Haun stage 5.0, for example, describes a wheat plant with 5 fully emerged leaves and a sixth leaf just at the point of emergence from the sheath. A plant with a Haun stage of 5.3 would have five fully emerged leaves and a sixth leaf that is 3 times the length of the fifth, fully emerged leaf. Plants were harvested as follows: eight plants were harvested at 28 d after emergence (trial 1) or six plants were harvested 24 d after emergence (trials 2 and 3).

Statistical analysis

All data were analyzed by ANOVA generating comparisons of the least significant difference (LSD) between means, based on student's t test.

Results and Discussion

One of the proposed mechanisms of the action of blue light is an enhancement or enabling of the action of phytochrome, thus it was important to try to eliminate the potentially confounding effect of the simultaneous action of phytochrome. According to the principle of equivalent action of light, two treatments creating the same photostationary state for phytochrome (ϕ) will have identical effects on a plant's responses caused by phytochrome (Sponga et al., 1986). Under these conditions, differences in plant response may then be ascribed to another photoreceptor or some other mechanism. Applying this principle to the blue light treatments in this study, the phytochrome photostationary states are nearly equal (ϕ = 0.81 for the high blue treatment, ϕ = 0.83 for the low blue treatment), so the blue-UV light receptor(s) becomes the probable causative agent for differences in plant response.

Effect of blue light on tillering

Wheat plants consistently produced more tillers when grown under 50 μmol m⁻² s⁻¹ blue light (normal MH lamp irradiation) compared with plants grown under 2 μmol m⁻² s⁻¹ blue light (filtered MH lamps). Plants produced an average of 25% more tillers under the higher level of blue light over three trials (Table 1). The difference in ϕ between the two
treatments was small and probably had only a negligible effect, if any, on tillering. In fact, the slightly lower ϕ in the high blue treatment would have been expected to result in fewer tillers, not more, as actually occurred (Barnes and Bugbee, 1991).

**Effect of blue light on dry-mass accumulation and leaf length**

Blue light did not significantly effect dry-mass accumulation (Table 2). To eliminate the possibly confounding effect of plant size on tiller production, we calculated tillers-per-plant and tillers-per-gram dry-mass (Table 3). Plants grown under high blue light consistently produced more tillers-per-gram of dry biomass than plants grown under the low level of blue light, which confirmed that the reduction in tillering was due to blue light, not a result of increased plant size. Leaf length (sheath plus lamina for longest emerged leaf) of plants grown under low levels of blue light was significantly longer than those grown under high levels (49.8 vs. 45.2 cm, P < .01).

**Effect of blue light on main culm development**

Main culm development (measured as Haun stage) was significantly enhanced by blue light in all three trials (Table 4). This result is somewhat surprising because it suggests the possibility that two different mechanisms of action may exist in wheat plants to mediate changes in main culm development in response to changes in blue light and phytochrome photoequilibrium. Our data indicate that high levels of blue light and higher values of ϕ, in general, tend to elicit the same morphological responses in wheat (Barnes and Bugbee, 1991). Tillering and leaf length, for example, were both increased by higher ϕ and higher levels of blue light, suggesting that the blue-UV light receptor(s) acts in concert with phytochrome in these responses. However, the response to higher blue light (more advanced Haun stage) in this study is opposite to the response to higher ϕ (less advanced Haun Stage).

Although it is possible that the difference in the phytochrome photoequilibria in the blue light treatments (ϕ = 0.81 for high blue and 0.83 for low blue) was responsible for the difference in Haun stage, it is unlikely that such a small difference in ϕ could cause the observed change. Our previous research (Barnes and Bugbee, 1991) demonstrated that reducing ϕ results in increased development of the main culm. Specifically, we found that reducing ϕ from 0.81 to 0.33 resulted in an increase of 0.5 Haun stage units. In the present case, a decrease in ϕ from 0.83 to 0.81 seems too small a change to be the sole cause of an increase of 0.2 Haun stage units. Also, at 0.83, ϕ is near its maximum value (about 0.89) and responses to changes in ϕ in that region of values have been shown to be negligible (Smith and Holmes, 1977).

The findings provide important insights to the mechanisms that control tillering in grasses. We did not attempt to predict ϕ gradients along the axis of the plant, which may be different from ϕ measured above the plant (see Casal and Smith, 1989). For example, because far-red radiation penetrates leaves and canopies much better than blue or red radiation, the predicted ϕ is probably different at the site of perception than above the plant. For these reasons, this study does not eliminate the possibility that the observed effect is mediated by phytochrome.

In addition, these findings have particular relevance to the selection of electric lamps for controlled environments. For example, only about 6% of the photosynthetic output of high pressure sodium lamps is between 400 and 500 nm (blue light). We plan to follow up this research with longer term studies that examine spectral effects on reproductive growth and final yield in widely spaced plants and in dense canopies.

### References


