

Morphological Responses of Wheat to Changes in Phytochrome Photoequilibrium¹

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ABSTRACT

Wheat plants (*Triticum aestivum* L.) were grown at the same photosynthetic photon flux (PPF), 200 micromoles per square meter per second, but with phytochrome photoequilibrium (φ) values of 0.81, 0.55, and 0.33. Plants grown at φ values of 0.55 and 0.33 tillered 43 and 56%, less compared with plants grown at φ of 0.81. Main culm development (Haun stage) was slightly more advanced at lower values of φ , and leaf sheaths, but not leaf lamina, were longer at lower φ . Dry-mass accumulation was not affected by different levels of φ . Three levels of PPF (100, 200, and 400 micromoles per square meter per second) and two lamp types, metal halide and high pressure sodium, were also tested. Higher levels of PPF resulted in more dry mass, more tillering, and a more advanced Haun stage. There was no difference in plant dry mass or development under metal halide versus high pressure sodium lamps, except for total leaf length, which was greater under high pressure sodium lamps (49.5 versus 44.9 centimeters, $P < 0.01$).

Tillering in grasses is affected not only by radiation quantity but also by its quality, or SED³, which affects the activity of at least two plant photoreceptors, the blue light receptor(s) and phytochrome (1–3, 9, 10, 16, 19). The characteristic SED of the radiation source determines the activity of each photoreceptor. Responses to blue light, for example, appear to be controlled by the absolute amount of blue light (400–500 nm) received by the plant. Phytochrome responses, on the other hand, are controlled by the ratio of the amount of phytochrome in the active form (P_{fr}) to the total amount of phytochrome (P_{total}), or P_{fr}/P_{total} (φ). This ratio (φ) in the plant can be predicted from the SED of the radiation source. Past research has relied mainly on an approximation of φ , called the ζ ratio, which is based on the relative amounts of radiation

at the peak absorption wavelengths for each form of phytochrome, generally considered to be centered around 660 nm for P_r and 730 nm for P_{fr} . However, exact values for these peak absorbances can vary, and different researchers have used ζ to represent a range of ratios (5, 7, 11, 17, 20, 26). In this paper, ζ represents the ratio of radiation at 660:730 nm unless otherwise specified.

Holmes and Smith (17, 25) characterized the relationship between ζ and φ for several natural and artificial radiation sources. They found that values for φ increased from a minimum of 0.04 to about 0.54 (typical sunlight φ) for corresponding ζ values of 0.05 and 1.15 (typical sunlight ζ), respectively. For ζ values from approximately 1.15 to 16, φ values asymptotically approached a maximum of about 0.75.

Investigations of the effect of different ζ ratios on tillering have mainly centered on the manipulation of ζ by irradiating plants with different artificial sources or by adding supplemental R or FR radiation to create ζ ratios higher or lower than sunlight. Casal *et al.* (5) exposed *Lolium multiflorum* (annual ryegrass) to red:far-red ratios (650:725 nm) of 1.62 and 0.84. The relative tillering rate in the lower ζ treatment ($\zeta = 0.84$) was reduced by half in vegetative plants and by one-third in plants that reached the reproductive stage; mean tiller number was reduced by 30%. In a later experiment, Casal *et al.* (8) found that reducing ζ from 1.44 to 0.62 again resulted in large reductions in tillering (from 24 to 14 tillers per plant), but as ζ was further reduced to 0.03, the number of tillers produced increased (from 14 to 19).

Deregibus *et al.* (11) altered ζ (650:725 nm) by adding R with light-emitting diodes at the base of *Paspalum dilatatum* Poir. and *Sporobolus indicus* (L.) R. Br. plants. They found that increasing this red:far-red ratio to twice that of sunlight (from 1.1 to 2.2) significantly increased tiller number in *P. dilatatum* (from 15 to 45) but not in *S. indicus*. Kasperbauer and Karlen (20) found that wheat tiller number decreased only slightly from 7.5 and 7.1 in response to a large decrease in ζ (645:735 nm) from 5.0 to 1.5.

Lower ζ ratios in dense canopies due to natural filtration by leaves (shading) appear to have the same effect as lower ζ ratios artificially created by manipulation of φ in controlled environments. Lowering of ζ by either means results in the morphological responses of increased stem elongation (17, 18, 24, 26) and reduced tillering (6, 20). Holmes and Smith (18) observed a significant increase in stem elongation in *Cucurbita pepo* L. and *Chenopodium album* grown in the shade of a simulated wheat canopy. Casal *et al.* (6) found a positive correlation between lowered ζ and reduced tillering

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³ Abbreviations: SED, spectral energy distribution; R, red light (650–700 nm); FR, far-red radiation (700–750 nm); P_{total} ($P_r + P_{fr}$), the total amount of phytochrome; φ (P_{fr}/P_{total}), ratio of the amount of phytochrome in the active form to total phytochrome; ζ , ratio of red to far-red irradiation, generally 660:730 nm; PPF, photosynthetic photon flux; HPS, high-pressure sodium; MH, metal halide.

in densely planted communities of *P. dilatatum* and *L. multiflorum*.

Direct *in vivo* measurement of phytochrome in etiolated plants (14, 18) has shown that changes in the ζ ratio affect φ . Unfortunately, this method cannot be used on mature green tissue because of the interference of Chl and other pigments, making it necessary to develop methods to predict φ from measurements of SED (14).

Because P_r and P_{fr} have absorption maxima near 660 and 730 nm, the most common method of estimating φ has been to use measurements of narrow wavebands of radiation centered around 660 and 730 nm (ζ) to predict φ . However, measurement of the output in these regions of the spectrum does not necessarily predict the same φ as measurement of all wavelengths of radiation affecting the interconversion of phytochrome. Because of this, we believe the ζ ratio is an inadequate estimate of φ , particularly for radiation sources that have spikes in their SED that may be unaccounted for in measurements of ζ . This may be especially true for those sources with a strong blue or near-UV component, because both forms of phytochrome have secondary absorption peaks in this region. Accordingly, we used the method of predicting φ developed by Gardner and Graceffo (14) and refined by Sager *et al.* (23) in which the intensity of radiation at each wavelength from 300 to 800 nm is measured, and the relative (estimated) amount of conversion of P_r to P_{fr} and P_{fr} to P_r at each wavelength is summed over the entire range of wavelengths to give the ratio of P_{fr}/P_{total} (φ).

Previous studies in this laboratory have indicated that wheat yields can be increased by reducing the number of late-forming tillers (4). The objective of this study was to reduce tillering of wheat by manipulating the SED of the radiation source. Such a reduction may help increase yield per day by allowing earlier harvest and by increasing the harvest index of the crop (4).

MATERIALS AND METHODS

Cultural Procedures

These experiments were conducted in a series of five trials. Each treatment contained 24 (trial 1) or 20 (trials 2–5) pots. Wheat (*Triticum aestivum* L., cv Fielder, cv Veery 10, and cv Yecora Rojo) seeds were sown into soilless media (equal parts peat moss, perlite, and vermiculite) in plastic pots (120 × 120 × 100 mm) and germinated at 23°C in a multisectioned, controlled-environment growth chamber. All plants in trials 1 to 3 were cv Fielder. In trials 4 and 5, 10 plants were cv Veery 10 and 10 were cv Yecora Rojo.

All sections of the growth chamber were connected to a common air-conditioning system; therefore, CO₂ concentration, humidity, and temperature were nearly identical. Temperature was continuously monitored with a shielded, type E, 24-gauge thermocouple in the center of each unit. Thermocouples were connected to a datalogger (Campbell Scientific Inc., model 21x). The average daily temperature was maintained at 21.5 ± 0.5°C in all sections throughout each trial. The atmosphere was enriched with CO₂ to approximately 1000 μmol mol⁻¹ to maximize the rate of assimilation. Plants were thinned to one plant per pot, 5 d after planting. All

plants were then of approximately equal size. Pots were rotated every 3 to 4 d to ensure uniform exposure to treatments. The planting density in each section, approximately 40 plants m⁻², was believed to be sparse enough to minimize the effect of reflected FR radiation (1). Pots were watered daily with about 300 mL of a dilute fertilizer solution (1:100 Peter's 20–5–30).

Spectral Treatments

In trials 1 and 2, two φ treatments with nearly identical total PPF (200 μmol m⁻² s⁻¹) were created. Plants in the control treatment were grown under white light ($\varphi = 0.81$) from a 400-W MH lamp (Sylvania) passing through a 5-cm water bath and 9-mm Plexiglas barrier (Dupont Lucite acrylic). Plants in the reduced φ (0.55) treatment were exposed to radiation from a 1000-W MH lamp (Sylvania) and two 500-W incandescent spotlights filtered as above and additionally filtered through a light blue (Rosco R64 "Light Steel Blue") filter (creating a $\varphi = 0.55$). In addition, three levels of radiation intensity (PPF = 100, 200, and 400 μmol m⁻² s⁻¹) were created in three separate sections of the growth chamber with 1000-W HPS lamps filtered through a 5-cm chilled water bath and 9 mm of Plexiglas and additionally filtered through layers of black neutral density screen to uniformly reduce PPF to the appropriate level. All HPS treatments created the same φ (0.85).

In trials 3, 4, and 5, three φ treatments were tested. Two of these were the same as in trial 1 ($\varphi = 0.81$ and 0.55). One additional reduced φ treatment was created by exposing plants to radiation from two 1000-W MH lamps (Sylvania) and three 500-W incandescent spotlights filtered through water and Plexiglas as described above and additionally filtered through a dark blue (Rosco R80 "Primary Blue") filter, creating a φ of 0.33 with a total PPF of 200 μmol m⁻² s⁻¹. HPS lamps and different radiation intensities were not tested in trials 3 to 5.

Radiation Measurements

Measurements of PPF and φ were made at the top of the plant canopy in each section. PPF was measured every 3 to 5 d throughout each trial. The height of plant trays was adjusted to maintain the appropriate PPF intensity at the canopy top. φ values were determined with a computer-driven spectroradiometer (Hewlett-Packard model HP-85 computer and an Optronics model 740 A spectroradiometer) using the method of Sager *et al.* (23). PPF and the relative contribution of blue photons to total PAR in each treatment were determined from the same spectroradiometric data. PPF data were corroborated with a quantum sensor (Li-Cor Inc., model LI-188B). Plants grown in white light ($\varphi = 0.81$) received 200 μmol m⁻² s⁻¹ of continuous PPF, of which 50 μmol m⁻² s⁻¹ was in the blue (400–500 nm) region of the spectrum. Plants in the reduced φ (0.55 and 0.33) treatments also received continuous PPF of 200 μmol m⁻² s⁻¹, of which approximately 67 and 117 μmol m⁻² s⁻¹ were in the blue, respectively. HPS lamp treatments (PPF = 100, 200, and 400 μmol m⁻² s⁻¹) received approximately 6, 12, and 25 μmol m⁻² s⁻¹ of blue light, respectively, creating a φ of 0.85 in each treatment.

Plant Measurements

At each harvest, tiller number, main culm development (Haun stage), and shoot dry weight (in grams) were determined. Haun stage is a measure of the development of cereal plants based on a comparison of the length of the latest leaf to emerge to the length of the previous leaf (15, 21). Harvest procedures were as follows: trial 1—eight plants were harvested from each treatment section at 23, 25, and 28 d after emergence; trials 2 and 3—eight, six, and six plants were harvested 16, 20, and 24 d after emergence; trials 4 and 5—five plants each of Veery 10 and Yecora Rojo were harvested 16 and 24 d after emergence. The lengths of the leaf sheath and lamina for each of the first five leaves were measured at each harvest.

RESULTS AND DISCUSSION

Effect of Radiation Intensity

Increased levels of PPF resulted in increased numbers of tillers produced (Fig. 1) and increased amounts of dry mass accumulated (Fig. 2), which is in agreement with the findings of Friend *et al.* (13). Tillering data are similar to the results of Evans *et al.* (12), who found that tiller number increased linearly with increasing solar radiation. Plants grown in the reduced φ treatments produced fewer tillers than would be predicted by irradiance alone (Fig. 1). To determine whether this effect was due to reduced φ or to some other cause, we compared dry-mass accumulation for all treatments tested and found dry mass to be a linear function of PPF intensity (Fig. 2, data shown are for trial 2 only). Plants grown in the reduced φ treatment, therefore, did not accumulate more dry mass in response to PPF than did plants grown in other treatments. The data in Figures 1 and 2, and previous research (13), also indicate that dry mass was positively correlated with tiller production; *i.e.* larger plants produced more tillers (Fig. 3). This was true for all treatments in trials 1 to 3, except for

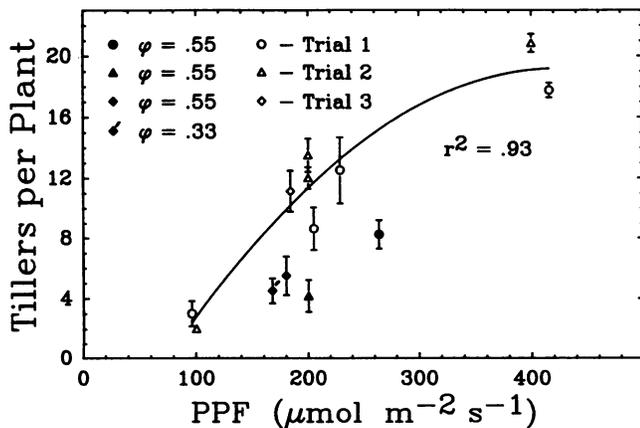


Figure 1. Tillering response of cv Fielder to increasing radiation intensity (PPF). Solid symbols, reduced φ treatments; not part of (2nd order) regression curves. Each data point, average of eight (trial 1) or six (trial 2 and 3) plants taken at the final harvest of each trial. Error bars, 95% confidence interval. Error bars that are smaller than the symbols do not appear.

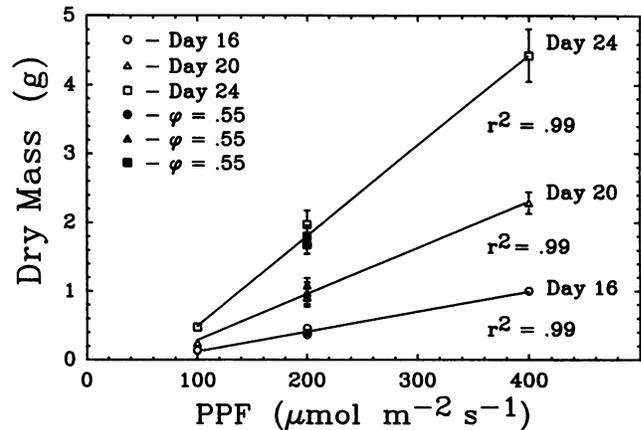


Figure 2. Dry-mass accumulation (in grams) as a function of increasing PPF. Each data point, average of eight, six, or six plants (cv Fielder) harvested 16, 20, and 24 d, respectively, after emergence (trial 2). Error bars, 95% confidence interval. Error bars that are smaller than the symbols do not appear.

the reduced φ treatments, which produced fewer tillers than would be predicted on the basis of dry-mass accumulation (determined by analysis of variance: $F = 9.76$, $P < 0.05$). These results suggest that the observed reductions in tillering cannot be attributed to differences in either irradiance or plant size and thus are assumed to be a photomorphogenic effect mediated by phytochrome.

Increasing irradiance also resulted in an increase in the development of the main culm (Haun stage), which confirmed the findings of Friend *et al.* (13). Plants exposed to lower φ increased their rate of main culm development more than would be predicted by PPF alone (Fig. 4).

Haun stage was reduced more rapidly at lower PPF levels (Fig. 4). This may be because development at low PPF is

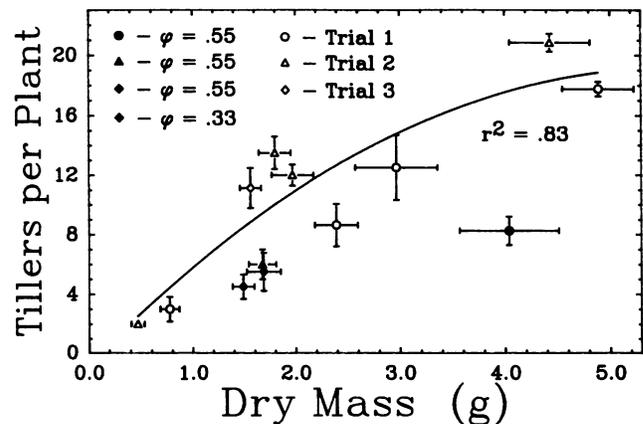


Figure 3. Tiller production as a function of dry mass. Data points are fitted to a 2nd order regression curve, except for the reduced φ values from each trial. Data points, averages of eight (trial 1) or six (trials 2 and 3) plants (cv Fielder) taken at final harvest. Error bars, 95% confidence interval. Error bars that are smaller than the symbols do not appear.

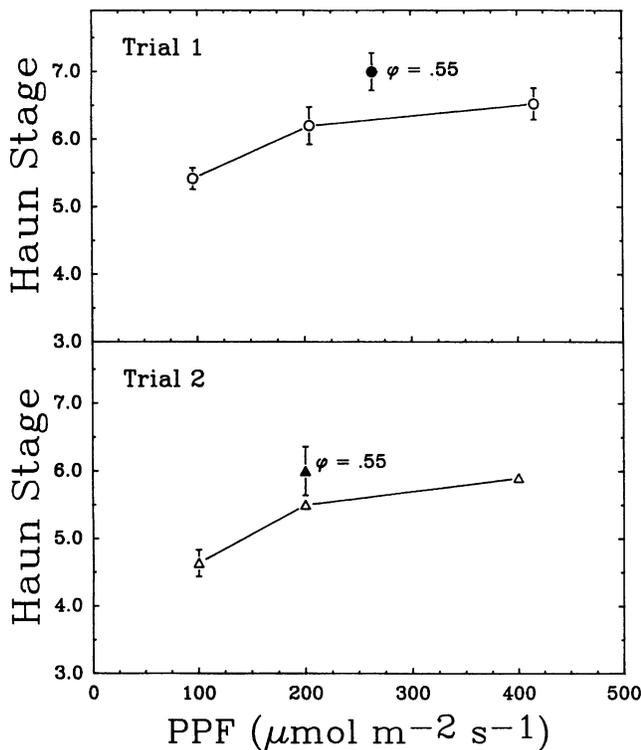


Figure 4. Effect of reduced ϕ on main culm development (Haun stage). Data points, averages of eight (trial 1) or six (trial 2) plants (cv Fielder) harvested 24 (trial 1) or 20 (trial 2) d after emergence. Error bars, 95% confidence interval. Error bars that are smaller than the symbols do not appear.

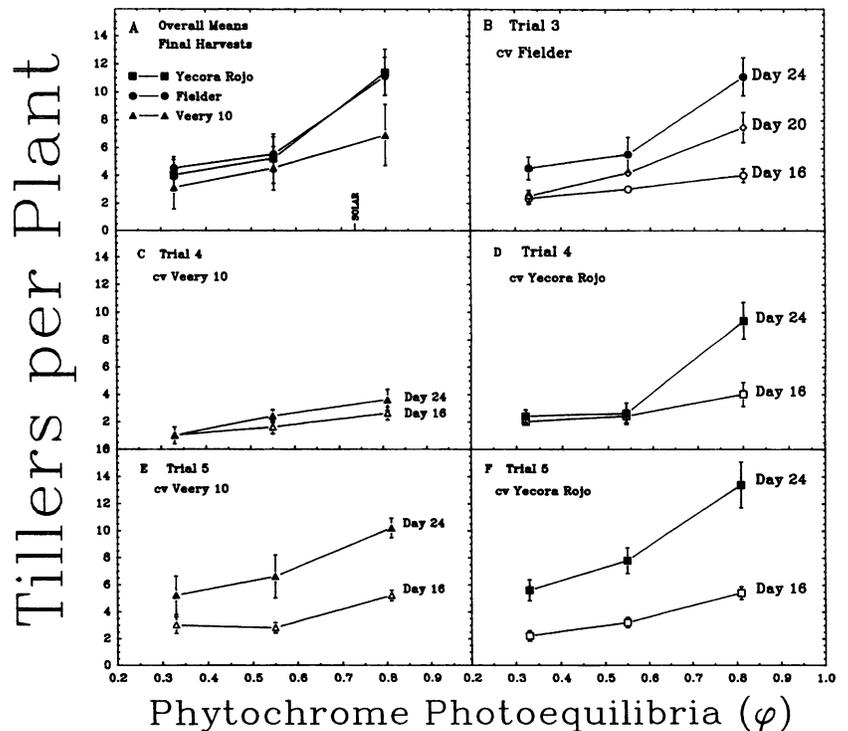
carbohydrate limited, thus development would stop at the light compensation point (about $50 \mu\text{mol m}^{-2} \text{s}^{-1}$).

Effect of Reduced ϕ

Changing ϕ from 0.81 to 0.33 reduced tiller number an average of 50% by the final harvest of each trial (Fig. 5A; $P = 0.0005$, significance determined by analysis of variance, $F = 49.1$, trials 4 and 5). The largest effect of ϕ on tiller production occurred between ϕ treatments of 0.81 and 0.55. There was a small additional reduction in tillering with a further reduction of ϕ to 0.33 (trials 3–5; Fig. 5). For cv Yecora Rojo and cv Veery 10 combined in trials 4 and 5, the average reduction in tillering was 47% for $\phi = 0.81$ and 0.55 ($P < 0.01$, based on LSD, Student's t test) and 27% for $\phi = 0.55$ and 0.33 ($P < 0.1$, based on LSD, Student's t test). Casal *et al.* (5, 8) studied the effect of phytochrome on tillering in *L. multiflorum* but based their findings on spectral measurements of ζ rather than ϕ .

Recent estimates indicate that the maximum possible ϕ and the value of ϕ for typical sunlight given by Smith and Holmes (17) are too low. Under irradiation with monochromatic R, the maximum possible ϕ *in vivo* may be as high as 0.89 (22); this upward revision of maximum ϕ increases the ϕ for sunlight to about 0.73 (23). Values for ϕ can, however, be estimated from their ζ . Values of ζ of 1.62 and 0.84 (5) correspond to ϕ values of about 0.74 and 0.59, respectively, and ζ values of 1.44 and 0.62 (8) correspond to ϕ values of about 0.70 and 0.53, respectively. These ζ thus approximate the ϕ values (0.81 and 0.55) used in this study. The tillering reduction in wheat of 47% in our study is consistent with the 30 and 41% reductions in *L. multiflorum* found by Casal *et al.* (5, 8). The much higher planting densities (123 m^{-2}

Figure 5. Production of tillers in response to changing levels of predicted ϕ . Data points, averages of six Fielder (trial 3) or five Veery 10 and Yecora Rojo (trials 4 and 5) plants from the final harvest of trials 3 to 5 (A); eight, six, and six plants at each of three harvests for cv Fielder (B); and five plants at each of two harvests for both Veery 10 (C and E) and Yecora Rojo (D and F). Error bars, 95% confidence interval. Error bars that are smaller than the symbols do not appear.



compared to 40 m^{-2} in our studies) used by Casal *et al.* (5) could act to reduce tillering, altering ζ by transmitting and reflecting more FR within the canopy. Also, Casal *et al.* (8) altered the ζ ratio by irradiating only the plant base with incandescent lamps, whereas we altered the φ of the radiation source above the plants.

Our results for very low φ , however, are substantially different from those of Casal *et al.* (8), who found an increase in tillering with ζ reductions <0.62 (similar to φ of about 0.53). Lower φ (which simulates deep shading) should result in an additional reduction in tillering. The increase in tillering with lower ζ (hence, lower φ), found by Casal *et al.* (8), is difficult to interpret, and this discrepancy was not addressed in their manuscript. The effect of reducing φ from 0.55 to 0.33 was less significant in our study (27% tillering reduction, $P < 0.1$) than the initial reduction from 0.81 to 0.55 (47% tillering reduction, $P < 0.01$), but the response is in the expected direction.

Of the three cultivars tested, cv Veery 10 tended to tiller less than cv Yecora Rojo and cv Fielder in all treatments. Surprisingly, cv Fielder, which was selected for this study because of its high tillering rate, tillered about the same as cv Yecora Rojo, a typically low tillering cultivar (Fig. 5).

Effect of Reduced φ on Leaf Extension

Leaf sheath and lamina length were measured for cv Veery 10 and cv Yecora Rojo in trials 4 and 5. The reduction in φ did not affect leaf lamina length in either cultivar tested in either trial (data not shown). The sheath length of early developing leaves increased slightly (about half of all leaf Nos. 1–3 tested increased, half showed no trend) with decreasing φ . Later developing leaves more clearly showed this trend, especially between φ treatments of 0.81 and 0.55 (Fig. 6). These results are consistent with the results of Casal *et al.* (7), who found that, although decreased ζ ratios increased sheath length of leaves in three species of grass, *L. multiflorum*, *S. indicus*, and *P. dilitatum*, only one of these species, *L. multiflorum*, increased lamina length in response to lower ζ .

Effect of Reduced φ on Haun Stage

A relationship between phytochrome and development rate has not been previously reported in grasses. In all three cultivars tested, reductions in φ resulted in a small, but consistent, increase in the rate of development (measured as Haun stage) over the range of φ values tested ($F = 56.5$, $P = 0.0004$, for trials 4 and 5). As with tillering, the main effect occurred between φ treatments of 0.81 and 0.55 ($P < 0.05$, based on LSD, Student's *t* test), with a less pronounced effect between $\varphi = 0.55$ and 0.33 ($P < 0.1$, based on LSD, Student's *t* test). In trials 4 and 5, the increase in Haun stage in response to lower φ was noticeable at day 16 (Fig. 7, B–C). In trial 3, the effect was observable at day 20 (Fig. 7A). Plants that increased in Haun stage in response to low φ treatments produced fewer tillers but just as much dry mass. These data, and those in Figure 4, suggest that plants exposed to lower φ may divert resources away from tillering to more rapid main culm development.

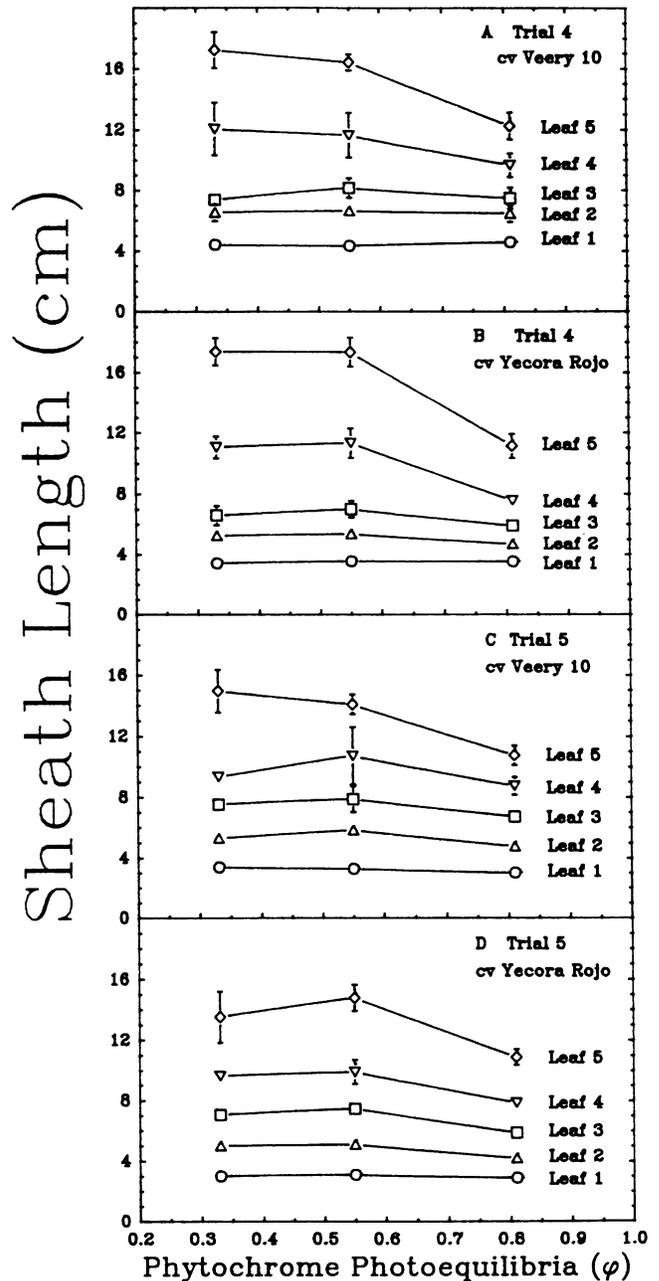


Figure 6. Sheath and lamina length (in centimeters) as a function of φ . Each data point, measurements of the first five emergent leaves of five cv Veery 10 and cv Yecora Rojo plants. Error bars, 95% confidence interval. Error bars that are smaller than the symbols do not appear.

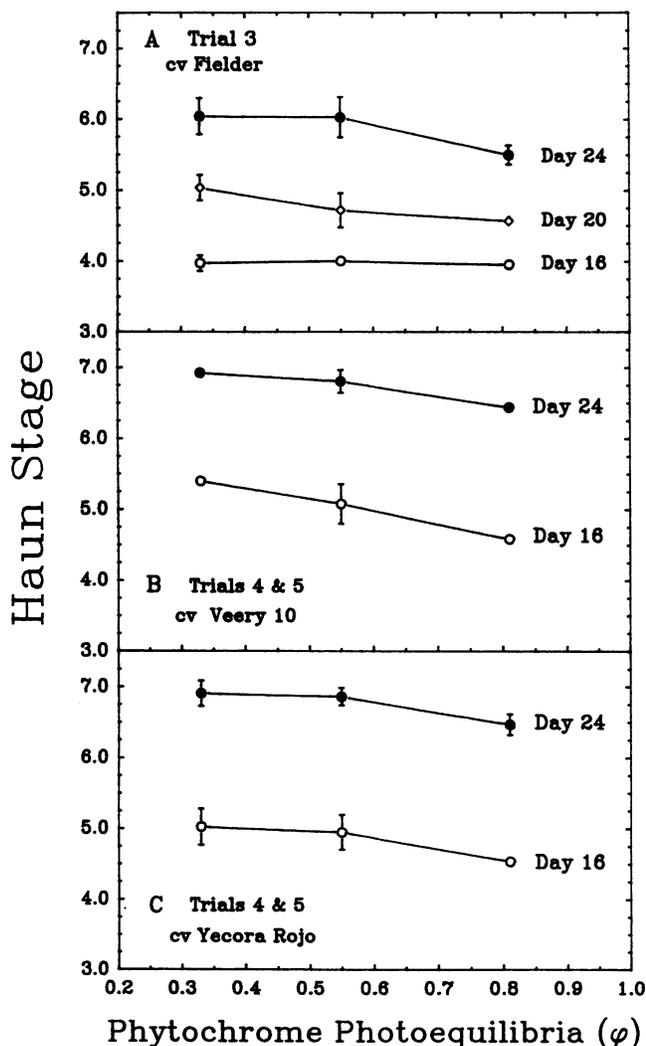


Figure 7. Main culm development (Haun stage) as a function of ϕ . Values for each data point for cv Fielder represent eight, six, and six plants for (trial 3) harvests at 16, 20, and 24 d after emergence (A). Each data point for cv Veery 10 (B) and cv Yecora Rojo (C) represents 10 plants: 5 from each of the final harvests (24 d after emergence) of trials 4 and 5 combined for each cultivar. Error bars, 95% confidence interval. Error bars that are smaller than the symbols do not appear.

Effect of Lamp Type on Wheat Morphological Responses

No difference was found in tiller number, Haun stage, or dry mass for wheat cv Fielder grown under HPS *versus* MH lamps at the same PPF ($200 \mu\text{mol m}^{-2} \text{s}^{-1}$) in trials 1 and 2. Leaves of plants grown under HPS lamps were, however, significantly longer ($P < 0.01$, based on LSD, Student's *t* test) than those grown under MH lamps (49.5 *versus* 44.9 cm).

Effect of Blue Light on Wheat Morphological Responses

Although the effects of blue light on wheat are the subject of a separate paper (in preparation), the possible complicating effects of blue light in the treatments being created in this

study need to be addressed. We have found that wheat responds to increasing amounts of blue light by producing more tillers, provided the phytochrome balance (ϕ) is held constant. For example, we found that increasing the amount of blue light from 2 to $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ increased tillering by 42% in wheat for two treatments in which ϕ values were approximately equal ($\phi = 0.81$ and 0.84). However, when ϕ is reduced and the amount of blue light is increased, as in the two reduced ϕ treatments in this study, these become competing or conflicting forces. The increasing blue light promotes more tillering in wheat, and the reduced ϕ acts to inhibit the same response. Wheat appears to be more responsive to reductions in ϕ than to the increased levels of blue light. Specifically, in the present study, there was a substantial reduction (>50%) in tillering associated with decreasing ϕ from 0.81 to 0.33, even though the amount of blue light in the same treatments increased from 50 to $117 \mu\text{mol m}^{-2} \text{s}^{-1}$. The response to reduced ϕ thus apparently overwhelms the response to blue light. This may be because the effect of blue light is saturated at fairly low fluence rates. Wheeler *et al.* (27) found that the effect of blue light on soybean height was saturated at $30 \mu\text{mol m}^{-2} \text{s}^{-1}$. At higher fluence rates of blue, there may be no additional effect.

Further research needs to be done to determine the relative importance of the blue light receptor(s) *versus* phytochrome in controlling plant responses, such as tillering.

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