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Research Article

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Response of giant foxtail and wild proso millet to artificial light quality alteration

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ABSTRACT

Light is an essential requirement for proper plant growth and development. Growth chamber experiments were conducted to determine whether artificial alteration of light quality (reducing the red to far-red ratio-R:FR) differentially affected the growth and development of giant foxtail and wild proso millet, two troublesome annual grass weeds in the United States. Growth phenotypes of both weeds were examined under two R:FR regimes (0.28-reduced R:FR and 1.12-unaltered R:FR) in the absence of competition (control conditions) and under intraspecific and interspecific competition. The reduced R:FR simulated shaded (below-canopy) R:FR conditions in the field while the unaltered R:FR treatment simulated direct sunlight (above-canopy) conditions. Averaged across weed species, reducing the R:FR increased plant height, but reduced tiller production and above-ground biomass under no plant competition ($P<0.05$). In the presence of competition, reducing the R:FR increased plant height and internode length but reduced the number of tillers and leaf area across weed species. No phenotypic differences were observed for weeds tested under intraspecific or interspecific competition. Our study has shown that the response of both weeds to artificial R:FR alteration is similar to that observed under shaded field conditions. Therefore, by replacing bordering plants with a crop, controlled experiments can be used to test the effect of crop canopies on weed suppression when selecting cultivars to be planted in areas where certain weed species are prevalent, minimizing weed-related yield losses.

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INTRODUCTION

Light is an essential requirement for proper plant growth and development. Important aspects of light affecting plant growth and development are the quantity of total energy (photosynthetically active radiation-PAR), spectral quality (R:FR), light duration, and photoperiod (Schmitt & Wulff, 1993). Changes in light quality can affect the development of shaded plants by influencing physiological processes mediated by phytochrome (Smith & Whitelam, 1990; Martínez-García *et al.*, 2010; Keuskamp *et al.*, 2010). Developmental responses mediated by phytochrome provide mechanisms for shade avoidance, which is accompanied by changes in plant phenotypes (Smith *et al.*, 1990; Smith & Whitelam, 1990; Pierik & de Wit, 2014; Carriedo *et al.*, 2016; Fiorucci & Fankhauser, 2017). Plants exhibit altered growth response (shade avoidance syndrome) due to reduced light availability by growth patterns such as taller stature, reduced branching or tillering, and lower biomass (Franklin & Whitelam, 2005; Pierik & de Wit, 2014; Carriedo *et al.*, 2016).

Giant foxtail (*Setaria faberi* Herrm.) and wild proso millet (*Panicum miliaceum* L.) are two problematic annual grass weeds that are predominant in the corn and soybean producing regions in the United States (Williams *et al.*, 2009; Cavers & Kane, 2016). The spread of giant foxtail and wild proso millet has been attributed to the ability to adapt to several environments, reproductive capabilities, and the ability to emerge throughout the growing season. Giant foxtail emerges earlier in the growing season (around the time of field corn emergence in the upper Midwest) than wild proso millet (Buhler *et al.*, 1997). However, wild proso millet is more dominant in field corn and sweet corn fields than giant foxtail. In field studies, giant foxtail and wild proso millet exhibited phenotypic changes under different sweetcorn canopy architectures, and weeds growing under the sweetcorn variety with a dense canopy had reduced tiller numbers, reduced biomass, lower population densities, and reduced seed production compared to the variety with an open canopy (Bisikwa *et al.*, 2021). The specific objective of this study was to determine whether giant foxtail and wild proso millet exhibited a differential response to artificially altered light quality (reduced R:FR) and whether this difference affected their growth and development and, thus, their competitive ability. We hypothesized that artificial alteration of the R:FR differentially altered phenotypic attributes of giant foxtail and wild proso millet. Controlled growth chamber experiments were conducted to test this hypothesis and examine the effect of reduced R:FR on plant phenotypes under no competition, intraspecific competition, and interspecific competition.

MATERIALS AND METHODS

Experimental Design

Experiments for this study were conducted across a 2-year period at the University of Minnesota in plant growth chambers maintained at alternating temperature (25 °C-day and 18 °C-night), a 16:8 hour day:night photoperiod, and 75% relative humidity. Plants in each growth chamber were illuminated by an overhead bank of 16 cool white fluorescent lamps (Phillips 72 inches) and 12 incandescent bulbs (60 watts). Two light conditions (R:FR regimes) were tested, i.e., 1.12-unaltered R:FR (simulating natural sunlight) and 0.28-reduced R:FR (simulating shaded conditions or reflected light in the field), with one growth chamber for each light level. To reduce the R:FR ratio in the other chamber to 0.28, radiation filters (blue spectral filters) were used to cover the incandescent bulbs to increase far-red radiation. The 0.28 R:FR light regime was set up one week after the emergence of both weed species (two weeks after planting) when weed species were at the first leaf stage. The set light conditions were maintained throughout the experiment. The set growth chamber temperatures facilitated uniform emergence of both weed species under respective light conditions and minimized potential confounding effects of different plant growth stage.

Experiments were set up as a split-plot design with four replications. Growth chambers were used as the main plots, and six weed species combinations (treatments) categorized into three groups (no competition, intraspecific competition, and interspecific competition) set up as sub-plots (the experimental design is summarized in Figure 1). Target plants were grown at the center of each 20-cm diameter plastic pot containing steam-sterilized soil for all treatment combinations. Treatment groups included: 1) No competition (controls)-target plants of each weed species without any bordering plants (Figure 1a, b); 2) Intraspecific competition-target plants of each weed species bordered by eight plants of the same species (GFGF-giant foxtail bordered by giant foxtail, and WPWP-wild proso millet bordered by wild proso millet) (Figures 1c, d and 3) Interspecific competition-target plants of each weed species bordered by eight plants of the other species (GFWP-

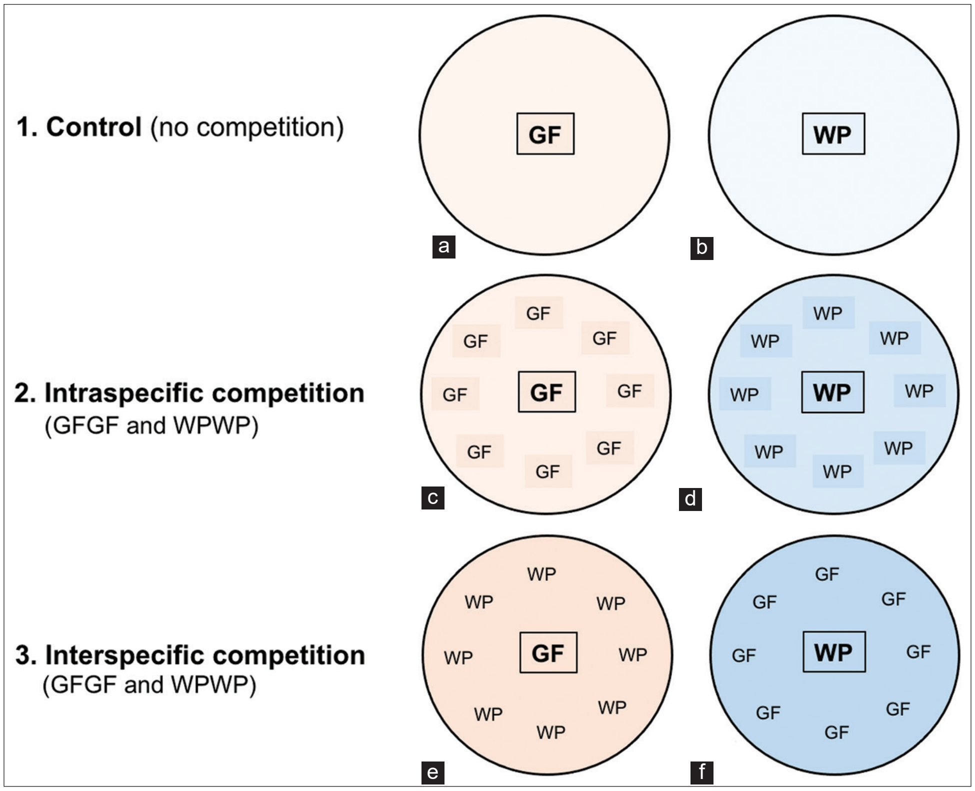

Figure 1: Experimental design (outer box represents the growth chamber, circles indicate pots and initials inside pots indicate plants of respective weed species). Target plants are located at the center of each pot. 1. Control (no competition), a) Giant foxtail (GF) b) Wild proso millet (WP). 2. Intraspecific competition, c) Giant foxtail bordered with giant foxtail (GFGF) and wild proso millet bordered with wild proso millet (WPWP). 3. Interspecific competition, e) Giant foxtail bordered with wild proso millet (GFWP) and f) wild proso millet bordered with giant foxtail (WPGF)

giant foxtail bordered by wild proso millet, and WPGF-wild proso millet bordered by giant foxtail) (Figure 1e, f). All bordering plants were located at an equidistant concentric arrangement 6 cm from the center target plant (Figure 1). After planting, pots were watered every three days throughout the experiment.

The R:FR was measured at the soil surface using a LICOR model 1800 spectroradiometer. Light quality was measured at 10 nm intervals between 400-800 nm with the LICOR 1800 equipped with a remote light collector on a fiber optic probe. A light spectrum was obtained for each growth chamber by measuring R:FR from direct radiation above the plant canopy. According to Smith (1982), the R:FR is defined as a ratio of radiation in the 10 nm bands centered on 660 and 730 nm. We used spectral irradiances at 660 and 730 nm to calculate the R:FR because they approach the peaks for phytochrome action spectra in green plants (Kasperbauer, 1987).

Data Collection and Analysis

In both growth chambers, data was collected for the center target plants throughout the experiment. Plant height and tiller numbers were measured weekly after light alteration. Plant height was measured from the base to the furthest extension of the uppermost part in its natural posture. Additionally, internode length, leaf area, and above-ground weed biomass of target plants were taken at the end of the experiment (approximately 16 days after light alteration and 30 days after planting). To measure internode length, leaf area, and above-ground biomass, all central plants were harvested, and all leaves stripped. Leaf area was estimated using a LICOR 3100 Area Meter. After leaf area measurements were taken, all above-ground biomass samples were oven-dried at 70 ^{o}C until a constant weight was reached (approximately three days). Data were tested for normality, and variances found to be homogeneous, and therefore, transformation was not necessary. During analysis, data for the two years were combined since there were no significant year by treatment interactions. Data were analyzed using one-way Analysis of Variance. For each measured phenotypic trait, the Fisher's Protected Least Significant Difference (LSD) test was used to determine differences between means and differences larger than the LSD considered significant at the 5% significance level.

RESULTS AND DISCUSSION

Exposure of weed seedlings to reduced R:FR (0.28) resulted in significant changes in plant height, number of tillers, leaf area, and above-ground biomass. Reduced R:FR ratio induced internode elongation (Tables 1 and 2), which in turn led to increased plant height (Figures 2a and 3a). Exposure of seedlings to reduced R:FR also led to reduced tiller numbers (Figures 2b and 3b).

Table 1: Phenotypic traits for the center target giant foxtail and wild proso millet plants under no competition

Treatment	Internode length (cm)	Leaf area (cm^2)	Above-ground biomass (g)
Light quality (average across species)			
R: FR (1.12)	5.9^b	1910^a	13.00^a
R: FR (0.28)	7.5^b	1529^a	10.25^b
LSD (0.05)	0.2	223	0.93
Species (average across light regime)			
GF	7.5^a	1537^b	9.33^b
WP	5.9^b	1902^a	13.92^a
LSD (0.05)	0.5	217	1.23

GF-giant foxtail; WP-wild proso millet. ^{a}All means are averaged across trial runs conducted in two years and means followed by the same letter within the same column do not differ significantly at P<0.05

Table 2: Phenotypic traits for the center target giant foxtail and wild proso millet plants under unaltered and reduced R:FR, and intraspecific and interspecific competition

Treatment	Internode length (cm)	Leaf area (cm^2)	Above-ground biomass (g)
Light quality (average across species)			
R: FR (1.12)	3.3^b	301^a	3.8^a
R: FR (0.28)	5.7^a	228^b	1.9^a
LSD (0.05)	0.1	42	1.06
Competing species (average across light regimes)			
Intraspecific competition			
GFGF	5.6^a	189^b	1.8^b
WPWP	3.7^b	330^a	3.7^a
Interspecific competition			
GFWP	5.3^a	185^b	1.9^b
WPGF	3.3^b	353^a	3.9^a
LSD (0.05)	0.4	24	0.30

GFGF-giant foxtail bordered by giant foxtail; WPWP-wild proso millet bordered by wild proso millet; GFWP-giant foxtail bordered by wild proso millet; WPGF-wild proso millet bordered by giant foxtail. ^{a}All means are averaged across trial runs conducted in two years and means followed by the same letter within the same column do not differ significantly at P<0.05

In a similar field study, Bisikwa *et al.* (2021) reported increased plant height, fewer tillers, and reduced above-ground biomass for giant foxtail and wild proso millet growing under a dense sweetcorn canopy with reduced R:FR compared to an open canopy. Averaged across weed species, reducing the R:FR increased plant height, but reduced tiller production and above-ground biomass under no plant competition ($P<0.05$) (Figure 2). Without competition, plant height increased by 53% for giant foxtail and 50% for wild proso millet under altered light compared to unaltered light. Averaged across light levels, giant foxtail had higher internode length, lower leaf area, and lower above-ground biomass compared to wild proso millet with no competition (Table 1). Across species, reducing the R:FR resulted in lower above-ground biomass (Table 1; Table 2). Examined over time (day 14 to day 30), giant foxtail had the tallest plants (Figure 2a) but the fewest tillers (Figure 2b) under reduced R:FR levels and no competition. However, wild proso millet had the shortest plants (Figure 2a) with the highest number of tillers under no competition (Figure 2b).

Under intraspecific competition, reduction of the R:FR induced internode elongation, which in turn led to increased plant heights for both weed species (Table 2, Figure 3a). Additionally, exposure of seedlings to the reduced R:FR ratio led to reduced tiller numbers for both weed species (Figure 3b). Our observations are consistent with previous studies that examined grass species. For instance, Skinner and Simmons (Skinner & Simmons, 1993) reported that in barley, enhancement of far-red light reduced the total number of tillers per plant while enhancing stem elongation. Consistent with our findings, Kasperbauer and Karlen (1994) also reported that corn seedlings grown under lower R:FR ratios developed longer stems and fewer tillers.

Generally, the response of giant foxtail and wild proso millet to altered light quality did not differ, i.e., the percent change in plant height or tiller number for giant foxtail and wild proso millet was similar when light quality was altered. In the environment with plant competition, plant height increased by 34% for giant foxtail and 35% for wild proso millet when grown under the reduced R:FR (0.28) compared to growth under unaltered light (R:FR=1.12). The presence of neighboring plants initiated shade avoidance responses in seedlings leading to shoot etiolation, reduced leaf area, and reduced above-ground biomass of center target plants (Table 2) compared to plants without any competition (Table 1) for both giant foxtail and wild proso millet ($P<0.05$). The presence of neighboring plants also increased ($P<0.05$) plant height (Figure 3a) compared to center target plants grown with no competition (Figure 2a). Tiller numbers were also reduced ($P<0.05$) for center target plants that had competition (Figure 3b) compared to those with no competition (Figure 2b). This occurred in both unaltered and reduced R:FR conditions. Similar findings were reported by Davis and Simmons (1994) in spring barley. Therefore, the plant responses observed in our study could be attributed to neighboring plants reflecting FR radiation, leading to FR enrichment. At the pot surface, R:FR averaged 0.20 and 1.00 after plant emergence for altered and unaltered chambers, respectively, while above the plants, R:FR was 0.28 and 1.12 for the two growth chambers. This drop in R:FR was only observed for plants undergoing competition with neighboring plants but not for single plants, in which case R:FR was 0.28 and 1.12 both at the soil surface and above the plants. The drop in R:FR at the pot surface in the presence of neighboring plants was plant-induced as plants further reflected FR light. Ballare *et al.* (1990) proposed that FR radiation from nearby leaves is a means of early detection of neighbors that signals oncoming competition during canopy development. Weed seedling responses to neighbors (competition) illustrate that plants may detect and developmentally respond to declines in R:FR associated with far-red light reflection from neighboring plants. For each weed species, the response of center target plants to interspecific competition with bordering weed plants did not differ ($P>0.05$) from that of intraspecific competition for all phenotypes measured in this study (Table 2). However, center target plants with neighboring plants growing under

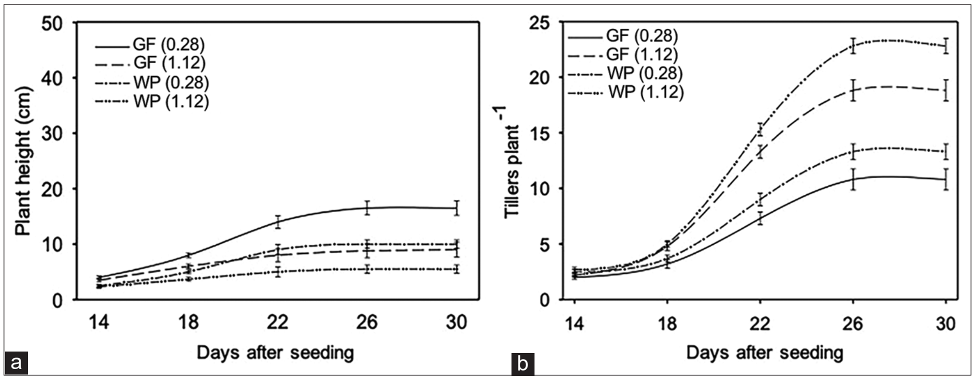

Figure 2: Effect of reducing the R:FR on average plant height (a) and tillers per plant (b) when the center giant foxtail (GF) or wild proso millet (WP) plant is grown with no competition from neighboring plants. Error bars indicate the standard error.

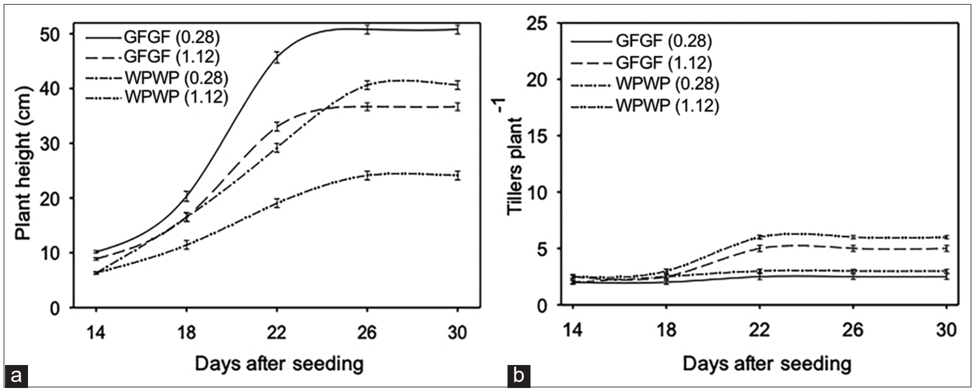

Figure 3: Effect of reduced R:FR on average plant height (a) and tillers per plant (b) when the center giant foxtail or wild proso millet plant under intraspecific competition. Error bars indicate the standard error. GFGF-giant foxtail bordered by giant foxtail, WPWP-wild proso millet bordered by wild proso millet.

reduced R:FR were more etiolated, had a lower leaf area, reduced plant height, fewer tillers, and had lower above-ground biomass compared with plants with neighbors grown under the unaltered R:FR (Table 2). This illustrates the influence of light quality on plant growth and development. Schmitt and Wulff (1993) showed that light quality controls developmental processes such as phototropism, photomorphogenesis, and photosynthesis.

At the low R:FR, seedlings of both weed species exhibited similar morphological responses compared to growth and development under unaltered light. Previous studies have reported that these responses are triggered by phytochrome in response to low R:FR ratios in the plant environment (Smith, 1982; Ballare *et* .,1990; Ballare *et* .,1991). The phytochrome system within the seedlings functioned as a sensor of competition and initiated physiological events that influenced prioritization in the allocation of new photoassimilates to the various components of the growing plants. The adaptive response of seedlings under reduced light R:FR (0.28) was to allocate more photosynthate for the development of longer stems, which increased the probability that the plants could establish some photosynthetic area above competing plants. When a greater fraction of photosynthate was allocated to elongating internodes and stems, less remained for tiller development, biomass production, and leaf expansion. Thus, the number of tillers per plant, total biomass, and leaf area was reduced as a consequence of reducing R:FR. Compared across light treatments, wild proso millet had 65% more leaf area, 67% more tillers, and 67% more above-ground biomass than giant foxtail. However, wild proso millet shoot internodes were 39% shorter, and shoots were, on average, 43% shorter than those of giant foxtail.

CONCLUSIONS

Our study has shown that the response of giant foxtail and wild proso millet to light quality alteration (R:FR reduction) is similar to that observed under shaded field conditions. Therefore, by replacing bordering plants with crop species, controlled experiments can be conducted to test the effect of crop canopies on weed suppression when selecting cultivars to be planted in areas where certain weed species are prevalent, minimizing yield reductions due to weeds. Weeds typically exist as multispecies communities, and it is important to understand changes in these adaptive morphological responses due to shifts in light spectral quality under canopies of competing plants. Knowledge of weed responses to light can enhance our understanding of how to manipulate the light environment in crop canopies to improve species-specific weed management in the field. This information may also be useful in predicting species shifts in response to changes in cultural weed management strategies.

COMPETING INTERESTS

The authors have declared that there are no competing interests.

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