

Shade avoidance cues reduce *Beta vulgaris* growth

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Abstract

Field and greenhouse experiments were conducted from 2013 to 2015 at the University of Wyoming to evaluate the response of *Beta vulgaris* (L.) to reflected-light quality. Large-pail field studies included a factorial arrangement of three varieties of *B. vulgaris* (sugar beet, table beet, and Swiss chard) and reflected-light treatments (using either colored plastic mulch, grass, or bare-soil controls). Greenhouse studies included sugar beet as influenced by either grass or soil surroundings. In all studies, grass was grown in separate containers from *B. vulgaris*, so there was no root interaction. Grass was clipped regularly to prevent shading and competition for sunlight. Reflected light from different-colored plastic mulches (red, blue, green, black, clear) did not affect *B. vulgaris* growth. However, reflected light from the grass reduced the number of leaves in all *B. vulgaris* varieties such that there were 10 to 14 fewer leaves in *B. vulgaris* surrounded by grass compared with the soil treatment at 90 d after planting in the field study. Shade avoidance cues from surrounding grass reduced *B. vulgaris* total leaf area by 49% to 66%, leaf biomass by 21% to 30%, and root biomass by 70% to 72%. Similar results were observed in greenhouse experiments, where the grass treatment reduced sugar beet leaf biomass by 48% to 57% and root biomass by 35% to 64%. Shade avoidance cues have the potential to significantly reduce *B. vulgaris* yield, even in the absence of direct resource competition from weeds.

Introduction

Most plants absorb light in the blue-violet region (400 to 500 nm) and in the orange-red region (600 to 700 nm) but transmit or reflect light in the far-red (FR) region (700 to 800 nm). Thus, light reflected from plant canopies has a reduced red (R) to FR ratio (R:FR). For example, the R:FR of daylight is about 1.19 compared with 0.13 for an ivy plant (*Hedera* spp.) (Smith 1982). The R:FR is a useful measurement of light quality in agricultural settings, because it relates to crops growing in weedy environments. Plants have evolved the ability to sense and respond to changes in the quality of light using a family of photoreceptors, particularly cryptochromes and phytochromes, which act as molecular switches in response to blue-violet light and R:FR ratio, respectively (Casal 2013).

Cryptochromes are blue and ultraviolet light receptors involved in perceiving blue to green light ratios (cryptochrome 1) or photoperiod (cryptochrome 2). Phytochromes exist as either R-absorbing phytochrome (Pr) or FR light-absorbing phytochrome (Pfr). When the stable form of the phytochrome (Pr) absorbs red light (660-nm peak absorbing wavelength), it converts to Pfr. The conformation change is reversible: under FR light (wavelengths neighboring 730 nm), the Pfr form of the phytochrome converts back to the Pr form (Hopkins and Huiner 2008).

Using this phytochrome transformation, plants can detect small changes in R:FR and initiate responses to avoid perceived impending competition. These responses range from growth and morphological changes, such as increased hypocotyl elongation, stem elongation, apical dominance and reduced branching (dicots), reduced tillering (monocots), and longer internode length, to physiological changes, such as assimilate distribution (Ballaré et al. 1990; Kasperbauer 1987; Smith 1992). These responses are collectively referred to as the “shade avoidance syndrome” (Roig-Villanova and Martinez-Garcia 2016). The ecological importance of shade avoidance responses is clear: by allocating more resources (photosynthates) to elongation growth, plants can overtop their neighbors and avoid being shaded in the future (Ballaré et al. 1987). However, this advantage comes with costs. Weinig and Delph (2001) demonstrated that when briefly exposed to low R:FR light, velvetleaf (*Abutilon theophrasti* Medik.) seedlings underwent stem elongation that had irreversible consequences on the plant’s ability to respond to environmental cues later in life.

Page et al. (2010) observed that corn (*Zea mays* L.) plants exposed to reflected FR light from early-emerging weeds set fewer kernels and allocated less biomass to the developing ear. In addition, corn plants exposed to reflected FR light had a reduced root-to-shoot ratio, making them more vulnerable to certain stress conditions such as drought or wind. In a related study, corn plants exposed to reduced R:FR, simulating early weed presence, had similar responses (Rajcan et al. 2004). Soybean [*Glycine max* (L.) Merr.] exposed to light reflected by neighboring weeds

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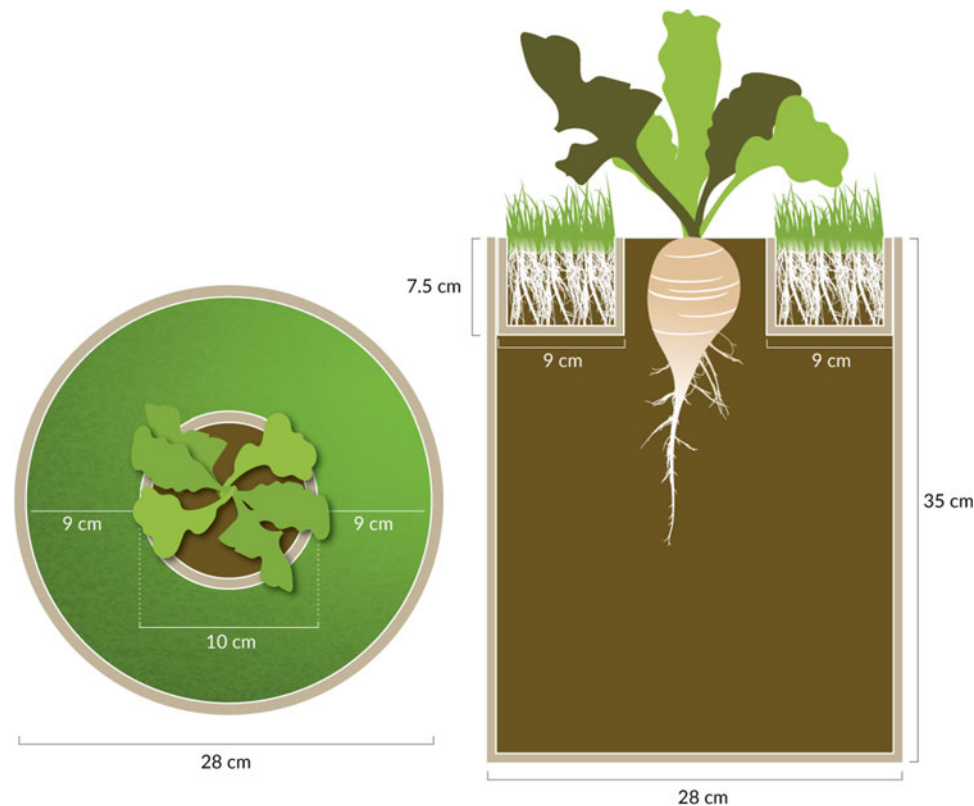


Figure 1. Illustration of the grass treatment used in the field experiment showing the top view (left) and a cross-section (right); modeled after Green-Tracewicz et al. (2011). *Beta vulgaris* was planted into the center ring and was allowed to grow using the full depth (35 cm) of the 21-L pail. Grass roots were constrained to the top 7.5 cm and outer 9 cm of the pail, and were isolated from the *B. vulgaris* roots using plastic. Grass was clipped as needed to minimize any direct shading of the *B. vulgaris* plant in the center. For the soil treatment, the design was the same, except no grass was planted into the potting media in the outer ring. Drawing by Jessica Perry.

showed elongated internodes, reduced branching, and reduced root-to-shoot ratio in the early stages of the plant compared with soybeans exposed to light reflected by bare ground (Green-Tracewicz et al. 2011). Apical dominance and increased stem extension are among the most common shade avoidance responses, as they offer plants a competitive advantage for light. Thus, for rosette-forming plants, shade avoidance responses may differ. For example, Vermeulen and During (2010) reported that a rosette-forming plant, creeping cinquefoil (*Potentilla reptans* L.), increased its petiole length when planted in high densities, although they did not specify whether the petiole elongation was correlated to the environmental R:FR ratio.

Beta vulgaris is physiologically a biennial species grown primarily as an annual crop for its sucrose-rich root, as in the case of sugar beet, but also as a root vegetable (table beet) or leafy vegetable (Swiss chard) (Winner 1993). The rosette growth habit of *B. vulgaris* makes it particularly sensitive to light competition (Dawson 1977; Schaeufele 1986; Zimdahl and Fertig 1967). In addition, the rosette growth habit would limit stem elongation (a typical shade avoidance response) in response to reduced R:FR. Thus, it is still unclear how a shade avoidance response might manifest in *B. vulgaris*. Shade avoidance responses precede resource competition and thus might influence the critical period of weed control in crops (Page et al. 2010). Understanding shade avoidance responses in sugar beet could aid in weed management decisions. The objective of this study was to evaluate the response of *B. vulgaris* to season-long reflected-light quality.

Materials and methods

Field experiments

Large-pail field studies were conducted in 2013 and 2014 to evaluate the response of *B. vulgaris* to reflected light. Three cultivars of *B. vulgaris*: sugar beet [*Beta vulgaris* ssp. *vulgaris* (L.), 'BTS 66RR60'], table beet [*Beta vulgaris* ssp. *vulgaris* (L.), 'Detroit Dark Red'], and Swiss chard [*Beta vulgaris* ssp. *vulgaris* (L.), 'Green Fordhook Giant'], were chosen for the study because of different physiology, resource allocation, and economic end products. As was noted earlier, sugar beet is grown for its sucrose-rich root, while table beet and Swiss chard are grown as root and leafy vegetables, respectively (Winner 1993). Thus, sugar beet and table beet partition most assimilates in the root, while Swiss chard partitions assimilates mostly into the leaves. In 2013, the study was a 3 by 6 factorial arrangement of three varieties of *B. vulgaris* (sugar beet, table beet, and Swiss chard) and five plastic mulch (Harris Seed Company, Rochester, NY) treatments (red, blue, green, black, clear colorless) and a nontreated control (bare soil). The experimental design was a randomized complete block (across irrigation line and east–west location gradient) with 15 replicates of each variety by mulch combination. This study used a modified container setup developed by Green-Tracewicz et al. (2011). The 19-L black plastic pails (35-cm height, 28-cm top diameter) were filled with peat and perlite potting media (Berger, BM Custom Blend, Saint-Modeste, QC, Canada), and the top was covered with the desired plastic mulch color. A 10-cm-diameter hole was cut into the plastic mulch

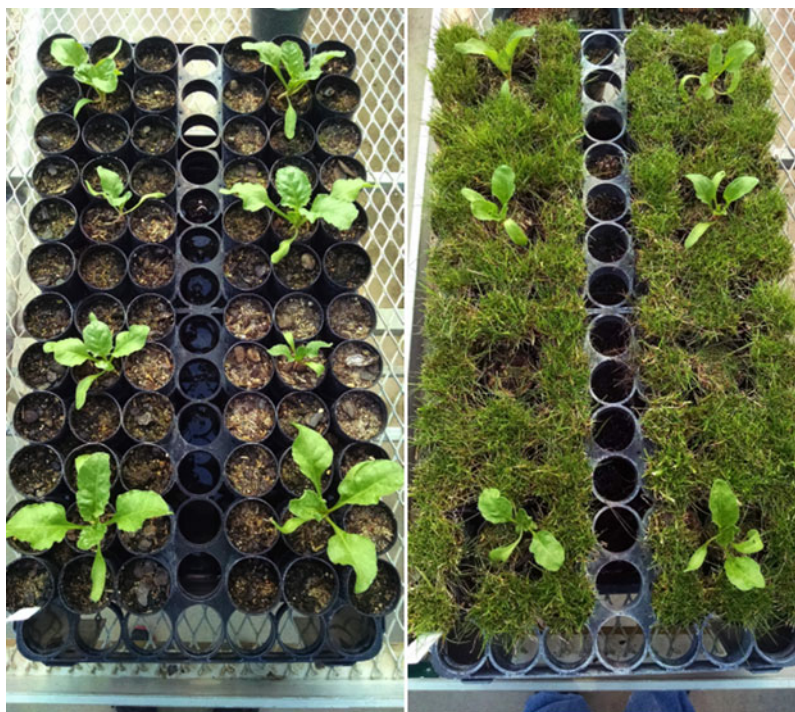


Figure 2. Greenhouse experiment setup. Each tray was one replicate (with 8 pseudo-replicates) and 28 × 58 cm in size. Each sugar beet was surrounded on all sides by cones either containing potting mix (bare-soil treatment, left) or planted with Kentucky bluegrass (grass treatment, right). Planting into separate cones ensured there was no below-ground interaction between sugar beet and grass.

in the center of the pail, and three *B. vulgaris* seeds were planted in the center of the hole on June 11, 2013. Shortly after emergence, each pail was thinned to a single *B. vulgaris* seedling.

In 2014, the study was a 3 by 6 factorial arranged in a randomized complete block design with 16 replications. The treatments included three cultivars of *B. vulgaris* (sugar beet, table beet, and Swiss chard) and six reflected-light treatments (black plastic mulch, three shades of green plastic mulch, grass to simulate a weedy environment, and bare soil to simulate weed-free conditions). This study used a modified container setup developed by Green-Tracewicz et al. (2011) to prevent any root interaction between the grass and *B. vulgaris* (Figure 1). The 19-L black plastic pails were filled with potting mix, leaving approximately 6 cm of headspace. A hollow cardboard ring (10-cm diameter, 7.5-cm depth) was placed in the center of the pail, and 0.15-mm-thick plastic was taped around the outside. Soil was then added on top of the plastic, filling the rest of the cardboard ring. Kentucky bluegrass (*Poa pratensis* L.) seed was planted at a high density in the outer ring (covered the entire surface of the outer ring) in the pails receiving the grass treatment 7 d before *B. vulgaris* was planted to ensure adequate grass growth at the time of *B. vulgaris* emergence. Squares (60 by 60 cm) of plastic mulch were stretched over the top of the pails receiving a plastic mulch treatment. Three *B. vulgaris* seeds were then planted in the center of the cardboard ring in each pail on June 6, 2014 and thinned to 1 seedling pail⁻¹ immediately after emergence (within 7 d after planting [DAP]). Because the ring was just 7.5-cm deep and there was no root impediment after the top 7.5-cm layer, the experimental setup allowed *B. vulgaris* plants to use resources in the entire 19-L pail, except for the area around the 7.5-cm-deep ring that was planted with grass or covered by plastic mulch. The grass was clipped regularly to ensure that the grass did not grow tall enough to shade

the crop. Also, the *B. vulgaris* and grass roots did not interact, and therefore, the effects of the grass treatment were limited to aboveground interactions like reflected light.

Pails were arranged in four rows spaced approximately 1 m apart. Within a row, pails were placed 25 cm apart to minimize reflected-light interference among experimental units. In 2013, pails were hand watered daily, and in 2014, *B. vulgaris* was drip irrigated daily until maturity to ensure no yield limitation due to moisture stress. The grass was also drip irrigated with a separate drip line to ensure green growth and maximal reflection of FR light. The irrigation methods used did not affect growth, because in both years, adequate moisture was applied throughout the season to prevent moisture stress. *Beta vulgaris* was fertilized with 30 g pail⁻¹ of 14:14:14:5.5% (N:P:K:S) polymer-coated fertilizer (Florikote™ NPK, Florikan ESA, Sarasota, FL) at planting to ensure slow and continuous release of nutrients throughout the growing season. Grass was not provided with fertilizer in addition to what was provided by the potting media; the grass remained a healthy green color for the duration of the season, so no supplemental fertilization was needed. Grass treatments were clipped regularly throughout the growing season to prevent direct shading of the *B. vulgaris* plants.

Reflected-light quality from the plastic mulches, grass, and bare soil was measured midseason (July 29, 2014) using a Jaz spectrometer (Ocean Optics, Dunedin, FL). Reflectance was measured from about 5 cm above the surface from all four cardinal directions and averaged to obtain reflectance per experimental unit. The R:FR of reflected light was calculated as the ratio of R to FR in the reflected-light spectra.

Following emergence, leaf number stage as described by Hohen (1998) was recorded for each *B. vulgaris* plant at 12, 22, 29, 35, 44, 52, 57, and 77 DAP in 2013 and at 18, 26, 34, 41, 48, 55, 69, and 89 DAP in 2014. Leaf stage describes the number of true leaves present

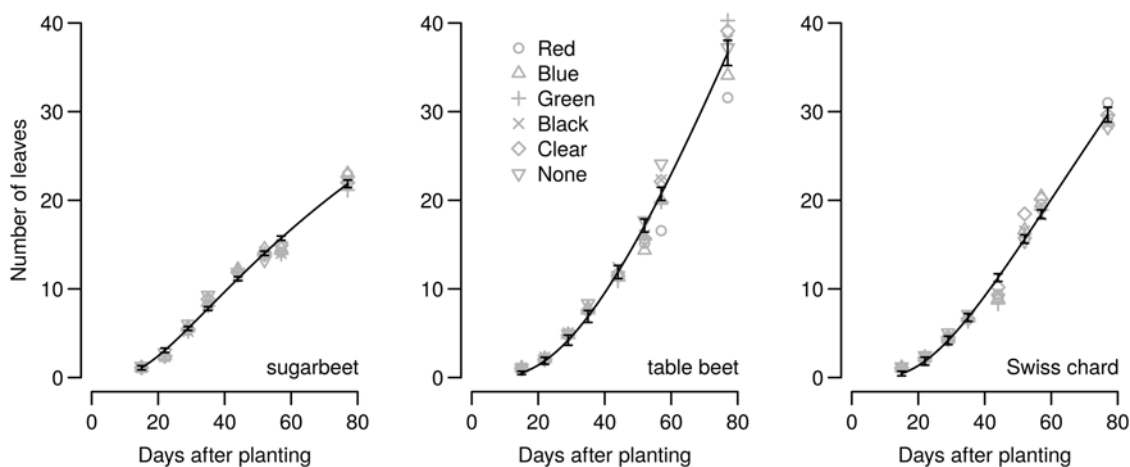


Figure 3. Effect of reflected light from colored plastic mulch on leaf number of *Beta vulgaris* varieties in 2013 field study, Laramie, WY. Regression equation and parameter estimates are provided in Table 1.

Table 1. Parameter estimates describing leaf number of *Beta vulgaris* varieties following the three-parameter Weibull model for the 2013 and 2014 field experiments, Laramie, WY.

Variety	Treatment	Parameter estimate (SE) ^a		
		<i>b</i>	<i>d</i>	<i>e</i>
2013				
Sugar beet	—	-0.69 (0.1)	91 (18.8)	128 (32.9)
Table beet	—	-0.44 (0.1)	1,993 (997.8)	1,758 (1056.7)
Swiss chard	—	-0.65 (0.1)	268 (126.0)	259 (136.8)
2014				
Sugar beet	Grass	-0.79 (0.4)	45 (33.9)	107 (95.0)
	Non-grass ^b	-0.70 (0.1)	108 (33.4)	168 (61.8)
Table beet	Grass	-1.52 (1.1)	18 (9.8)	45 (18.1)
	Non-grass	-0.77 (0.2)	122 (79.0)	157 (111.2)
Swiss chard	Grass	-0.63 (0.8)	62 (153.5)	165 (552.6)
	Non-grass	-0.47 (0.1)	911 (482.7)	1,225 (792.2)

^a $Y = d^* - \exp\{b^* [\log(x) - e]\}$. Parameter estimates are described in text preceding Equation (1).

^bSoil plus colored plastic mulch treatments.

and includes the percentage of development of the newest leaves, if they are not fully developed.

All plants were harvested on August 26 to 27 in 2013 and September 3 to 4 in 2014. In 2014, root length, diameter, and fresh weight were measured in table beet and sugar beet at harvest. Diameter was measured at the widest part of the root using a digital caliper, and length was measured from the crown of the root to the root tip. Total leaf area per plant was measured using a Delta-T Leaf Area Meter (Delta-T Devices, Cambridge, UK). Leaf dry weight was measured after leaves had been dried for 48 h at 60 C.

Greenhouse experiment

A greenhouse experiment was conducted twice in 2015 to evaluate shade avoidance responses in sugar beet under controlled environmental conditions. There were two treatments: grass (to simulate a weedy environment) and bare soil (simulating weed-free conditions) arranged in a randomized complete block design with four

replications (Figure 2). Each cone tray measuring 28 by 58 cm was considered a block (Figure 2). There were 8 sugar beet (pseudo-replicates) per block. Three sugar beet seeds were planted in February 2015 (first run) and in April 2015 (second run) in individual 158-ml cones (21-cm deep, 4-cm in diameter) and thinned to 1 seedling per Cone-tainer™ immediately after emergence. Each sugar beet was surrounded by either cones containing potting mix (bare-soil treatment) or planted with *P. pratensis* (grass treatment), as illustrated in Figure 2. In the first run of the experiment, sugar beet and grass were subirrigated by immersing the bottom 5 cm of each Cone-tainer in plastic trays filled with water. In the second run, the sugar beet and grass was watered twice daily by hand using an overhead sprinkler. Sugar beet leaf number as described by Holen (1998) was recorded at 7- to 10-d intervals after emergence. Plants were harvested at 47 DAP (first run) and 55 DAP (second run), and the number of leaves, leaf fresh and dry weights, and root fresh and dry weights were measured.

Data analysis

Nonlinear regression analysis was performed using the drc package (v. 3.0-1) in the R statistical language (v. 3.4.4) to quantify the effect of light environment treatment and *B. vulgaris* variety on leaf number over time (R Core Team 2016; Ritz et al. 2015). A three-parameter Weibull model was used (Equation 1), where *Y* is the number of *B. vulgaris* leaves at time *x*, *d* is the upper-limit asymptote, *x* is time in days after planting, *e* is the value of *x* at the inflection point on the curve, and *b* is a slope parameter. The Weibull model provides appropriate statistical parameter estimates of plant growth with meaningful biological interpretations (Shafii et al. 1991). For the 2014 field study, the number of true leaves for each variety and each light environment treatment was estimated from the model, and 95% confidence intervals were calculated.

$$Y = d^* - \exp\{b^*[\log(x) - e]\} \quad [1]$$

Harvest data (leaf area, leaf biomass, and root biomass) were analyzed with ANOVA in the R statistical language (v. 3.4.4), and treatment mean differences were separated using Fisher's protected LSD at alpha = 0.05.

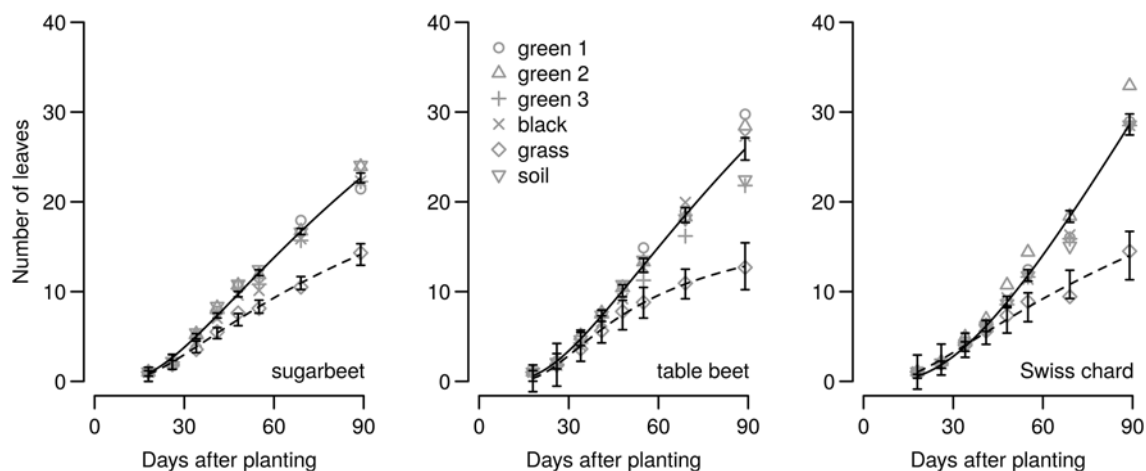


Figure 4. Effect of reflected light from bare soil, grass, and colored plastic mulch on leaf number of *Beta vulgaris* varieties in 2014 field study, Laramie, WY. Regression equation and parameter estimates are provided in Table 1.

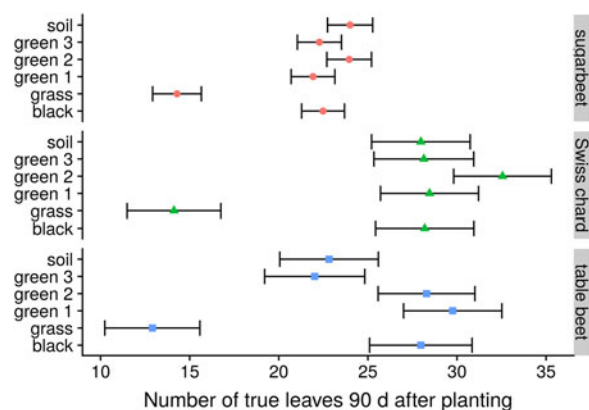


Figure 5. Effect of reflected light from grass and colored plastic mulch on leaf number of *Beta vulgaris* varieties in at 90 d after planting in 2014 field study, Laramie, WY. Bars represent 95% confidence intervals of the estimates.

Results and discussion

Reflected light from different-colored plastic mulches did not affect *B. vulgaris* leaf number in field studies conducted in 2013 (Figure 3; Table 1) or 2014 (Figure 4; Table 1). The R:FR of reflected light from the grass canopy was 0.66 compared with black (1.15) or green (1.16 to 1.55) plastic mulches and the bare soil (1.11). The R:FR values observed for non-grass treatments in this study were similar to the 1.0 and 1.18 for gray-white and brick-red soil surfaces reported by Kasperbauer and Karlen (1994) and similar to the 1.19 of daylight observed by Smith (1982).

In the 2014 field study, the grass treatment substantially reduced leaf number in all *B. vulgaris* varieties compared with control or plastic mulch treatments (Figure 4), so that by 90 DAP, there were 10 to 14 fewer leaves in *B. vulgaris* surrounded by grass compared with *B. vulgaris* in the soil treatment (Figure 5). Craig and Runkle (2013) have shown that shade avoidance responses (e.g., stem elongation) can be initiated at R:FR as low as 0.66. This supports the assertion that reduced leaf number in the grass treatment was due to the reduced R:FR, as the effect was not observed for any of the plastic mulch colors, which had a negligible effect on R:FR. In the 2014 field studies, grass treatments increased the time required to reach 6 true leaves by 7, 4, and 3 d compared

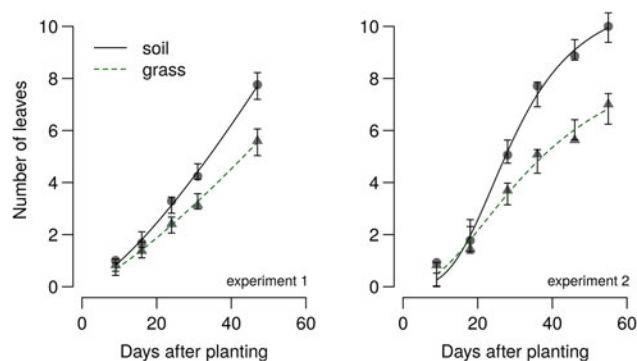


Figure 6. Effect of reflected light from grass on sugar beet leaf number in 2015 greenhouse study, Laramie, WY. Regression equation and parameter estimates are provided in Table 2.

with soil in sugar beet, table beet, and Swiss chard, respectively (Figure 4). Similar results were obtained in greenhouse studies, where grass increased the time to reach 6 true leaves by 11 to 15 d (Figure 6; Table 2). Previous studies in corn have shown that reflected FR from weeds increased stem elongation and reduced the number of visible leaf tips (Page et al. 2009, 2011). Thus, the reduction in the number of *B. vulgaris* leaves might be due to increased allocation to other plant parts.

Differences in sugar beet leaf number were observed after 30 DAP, which corresponded with the appearance of 4 to 8 true leaves (Figures 4 and 6). The difference in leaf number at this stage of development could be due to the transition from leaf canopy-dominated growth to root cambium development (followed by storage root and sugar accumulation-dominated phase). This is because the sixth to seventh cambia, which contribute to the bulk of storage root size and weight, are laid down by the 6-true leaf stage in sugar beet (Milford 2006). The difference in leaf number at early growth stages of *B. vulgaris* suggests that shade avoidance responses in *B. vulgaris* can be initiated early in the growing season, but responses later in the growing season need to be investigated. Thus, early-emerging weeds might reduce growth and yield even in the absence of direct resource (light, water, and nutrients) competition or depletion.

Reflected FR light from grass reduced leaf biomass and leaf area at harvest in all three *B. vulgaris* varieties ($P < 0.001$) and root

Table 2. Parameter estimates for sugar beet leaf number following the three-parameter Weibull model for 2015 greenhouse experiments, Laramie, WY.

Experiment	Environment	Parameter estimate (SE) ^a		
		<i>b</i>	<i>d</i>	<i>e</i>
Run 1	Soil	-1.3 (0.12)	284 (1,036)	646 (1,885)
	Grass	-1.2 (0.15)	230 (1,004)	828 (3,032)
Run 2	Soil	-3.2 (0.51)	11 (0.94)	30 (2.0)
	Grass	-2.1 (0.57)	10 (2.6)	36 (10.3)

^a $Y = d * -\exp\{b * [\log(x) - e]\}$. Parameter estimates are described in text preceding Equation (1).

Table 3. Effect of reflected light from grass on sugarbeet, table beet, and Swiss chard leaf biomass, leaf area, and root biomass at 90 d after planting in 2014, Laramie, WY.^a

Variety	Environment	Leaf biomass —g—	Leaf area —cm ² —	Root fresh weight —g—	Shoot: root biomass
Sugar beet	Soil	44	12,553	288	0.64
	Grass	31*	4,684*	85*	1.54
Table beet	Soil	34	6,859	188	0.76
	Grass	27*	2,307*	52*	2.27
Swiss chard	Soil	43	11,010	—	—
	Grass	34*	5,613*	—	—

^aMeans followed by an asterisk (*) are statistically different from the same variety grown in a soil environment according to Fisher's LSD ($\alpha = 0.05$).

^bRoot fresh weight was reduced by 76% to account for average moisture content before calculating shoot:root biomass. Because this variable was calculated from treatment means, no statistical analysis was performed.

biomass in sugar beet and table beet ($P < 0.001$) in the 2014 field study (Table 3). The grass treatment reduced *B. vulgaris* leaf biomass by 21% to 30%, leaf area by 49% to 66%, and root biomass by 70% to 72% compared with the soil treatment. Similar results were observed in the greenhouse study, where sugar beet leaf biomass was reduced by 48% to 57% and root biomass by 35% to 64% in the grass treatment compared with the soil treatment (Table 4). Reduction in leaf area and biomass are common shade avoidance responses. Reduced R:FR resulting from reflected FR light reduced leaf area and biomass in corn (Page et al. 2009, 2010, 2011), and leaf area, leaf, root, and total biomass in soybean (Green-Tracewicz et al. 2011). The reduction in *B. vulgaris* leaf area was primarily a function of fewer leaves being produced in the grass treatment. Similarly, the fewer leaves and the concomitant reduction in leaf area likely resulted in reduced *B. vulgaris* root biomass.

If 76% moisture content of root fresh weight is assumed (McGrath and Trebbi 2007), then shoot-to-root biomass ratio in the 2014 field study was 0.64 to 0.76 for the soil treatment compared with 1.54 to 2.27 for the grass treatment (Table 3). In a related study, Rajcan et al. (2004) similarly observed greater shoot-to-root ratio in corn due to reduced R:FR. The optimality hypothesis suggests that plants allocate more resources to the part that is acquiring the resource that is currently the most limiting (Reich 2002; Thornley 1972). Thus, perceived impending light competition from plant-reflected light results in more allocation to aboveground plant parts (Poorter et al. 2012). This is especially

Table 4. Effect of reflected light from grass on sugar beet leaf and root biomass in 2015 greenhouse study, Laramie, WY.

Treatment	Biomass —g plant ⁻¹ —			
	Study 1		Study 2	
	Leaf	Root	Leaf	Root
Soil	0.3	0.23	0.31	0.17
Grass	0.13	0.082	0.16	0.11
P-value	<0.001	<0.001	<0.001	0.064

problematic in root crops like sugar beet and table beet, because the roots are the primary economic product.

The reduction in root biomass observed here shows that shade avoidance responses have the potential to reduce root yield of sugar beet and table beet even in the absence of resource depletion by weeds. Similarly, leaf yield of Swiss chard might be reduced by shade avoidance responses. However, it is unclear what the total magnitude of these shade avoidance impacts may be in a production setting, because weeds are typically removed multiple times during the growing season. The effects of shade avoidance responses on leaf and root yield under typical growing conditions are almost certainly less than the magnitude observed in this study, in which the shade avoidance signal was allowed to persist from *B. vulgaris* germination until harvest. But it is also currently unclear how much of the yield loss due to shade avoidance cues is reversible after weeds have been removed. For example, how much yield potential (if any) is sacrificed during the time from *B. vulgaris* emergence until the 2-true leaf stage when weeds are commonly removed? Future research should explore the relationship between shade avoidance and the critical period of weed removal in *B. vulgaris*.

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