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Article

Light Reflected from Different Plant Canopies Affected Beta Vulgaris Growth and Development

Albert T. Adjesiwor[1]^*, Andrew R. Kniss[1,]

[1] Department of Plant Sciences, University of Wyoming, Laramie, WY, 82071 USA;
^A.T. Adjesiwor's present address: University of Idaho, Kimberly Research and Extension Center, Kimberly, ID, 83341
* Correspondence: aadjesiwor@uidaho.edu; Tel.: +1 208-423-6616

Abstract: Studies on crop response to light quality [red (R) to far-red (FR) light ratio] often recommend early weed removal to reduce the effects of shade avoidance responses on crop yield. However, it is unclear whether crops are able to distinguish reflected light quality of kin from that of non-kin. We evaluated the response of sugarbeet (*Beta vulgaris* L.) to reflected FR light from sugarbeet, common lambsquarters (*Chenopodium album* L.), Kentucky bluegrass (*Poa pratensis* L.), alfalfa (*Medicago sativa* L.), and bare soil (control) under outdoor conditions in 2016 and 2017. Treatments were completely randomized with 10 replications per treatment. The study methods ensured there was no direct resource competition. The reflected R:FR of plant species ranged from 0.06 (common lambsquarters) to 0.24 (sugarbeet) compared to 0.7 for the bare soil. In both 2016 and 2017, there were 2 to 4 more leaves in the sugarbeet surrounded by soil compared to sugarbeet surrounded by neighboring species. There was up to 47, 57, 43, and 23% reduction in sugarbeet leaf area, shoot dry weight, root diameter, and root dry weight, respectively, due to reflected R:FR light from neighboring species. Sugarbeet did not respond differently to reflected light quality of kin compared to non-kin.

Keywords: far-red light, kin recognition, light quality, shade avoidance, weed competition

1. Introduction

Competition among plants arises due to the limited availability of nutrients, water, and light [1]. Plants, though sessile, are not passive. Immobility has made plants evolve mechanisms for detecting neighbor proximity and initiate responses to enable them to compete for resources [2]. Proximity detection is particularly important in the competition for light because light serves as the primary source of energy for photosynthesis in plants. Through photoreceptors (e.g., phytochromes and cryptochromes), plants are able to sense the quality of light (particularly red (R) to far-red (FR) ratio) and use this as a cue to perceive the proximity of neighbors and impending competition for light. Green vegetation absorbs R and reflects much of incoming FR light and thus, neighbor proximity often reduces R:FR. In response to reduced R:FR, plants tend to elongate their hypocotyl, stem, and petioles; decrease rate of leaf expansion; and flower early [3]. These responses are collectively referred to as the shade avoidance syndrome [3,4].

This phenomenon has been widely studied as it affects growth and yield of crops [5-9]. Most studies on shade avoidance evaluated the effects of reflected light quality from heterospecifics (different species) on crop growth and yield [5,9,10]. Since reflected light from all green vegetation has a reduced R:FR, it will be of interest to know if crops are able to distinguish reflected light quality of kin (kin recognition) from that of non-kin such as weeds. Kin recognition, or the ability to "discriminate between related and unrelated individuals" [11], has been relatively less studied in plants compared to animals. Most kin recognition studies in plants focused on root interactions and resource competition or volatile compound signals [12-16]. Also, results from photoreceptor-mediated kin recognition studies are not consistent. For example, Crepy and Casal [17] and Crepy and Casal [18] observed that Arabidopsis thaliana recognized kin and reoriented leaves more horizontally when grown with kin than when grown with non-kin. They elucidated that the response involved the perception of R:FR and blue light. However, de Wit, et al. [19] reported that in rosette-forming plants such as A. thaliana, physical touching of leaf tips might precede R:FR sensing for neighbor detection. Thus, neighboring species architecture may influence shade avoidance responses.

Robson, et al. [20] stated that rapid stem expansion often observed at high crop densities is an "agriculturally wasteful allocation of assimilates to stem growth". Photoreceptor-mediated kin recognition is important because studies on shade avoidance recommend early weed removal as a management strategy for reducing the effects of shade avoidance on crop yield [7,21,22]. Thus, in the absence of weeds, it could be useful for plants to be able to distinguish light quality of conspecifics from that of heterospecifics to prevent yield loss due to shade avoidance. The specific question we seek to answer is, can sugarbeet differentiate reflected light quality of kin (sugarbeet) from non-kin (non-sugarbeet)? In a recent review, it was argued that current environmental and land-use conditions may necessitate planting crops at higher densities to increase crop yields [3]. In fact, it was posited that optimizing shade avoidance responses may be important for increasing crop yields at high planting densities [23]. Since kin recognition may be density-dependent [24], understanding crop response to reflected light quality from conspecifics and heterospecifics is important. This study, therefore, evaluated the response of sugarbeet to reflected light quality from kin and non-kin.

2. Materials and Methods

2.1 Site description, treatments, experimental design, and data collection

Studies were conducted in 2016 and 2017 at the University of Wyoming Laramie Research and Extension Center, Laramie WY to evaluate the response of sugarbeet to reflected light quality from different species. The experiment comprised four neighboring species (sugarbeet, common lambsquarters (Chenopodium album L.), Kentucky bluegrass (Poa pratensis L.), alfalfa (Medicago sativa L.)) and a bare soil (untreated check) treatment arranged in a completely randomized design with 10 replicates. Species were selected to ensure that not all species were closely related to sugarbeet while ensuring different functional groups were present. The study setup ensured there was no resource competition (Figure 1). Neighboring species were planted at high densities to ensure that there was full coverage of soil surface for maximal FR reflection. Three seeds of sugarbeet (cultivar "BTS60RR27" and "RR014GEM50" in 2016 and 2017, respectively) were planted per pot and thinned to one seedling per pot immediately after emergence. Sugarbeet was planted after neighboring species have emerged to ensure there was reduced R:FR at the time of sugarbeet emergence. Sugarbeet and neighboring species were drip irrigated daily to ensure water was not a limiting factor. Sugarbeet was fertilized with 40 g of 14:14:14:5.5% (N:P:K:S) polymer-coated fertilizer at planting to ensure a slow and continuous release of nutrients throughout the growing season. The inner pail (Figure 1) was either raised or neighboring species clipped regularly to prevent direct shading and competition for sunlight.

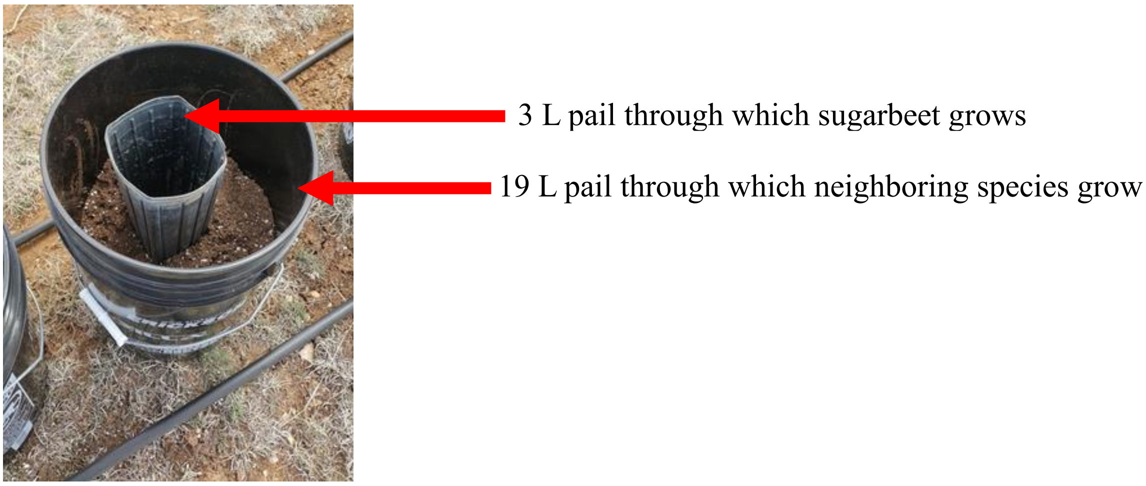

Figure 1. Experiment setup ensuring there was no resource competition. This setup made it possible to raise the inner pail when necessary to prevent direct shading of sugarbeet

The spectral signature of the four species and the bare soil surface were measured using a FieldSpec4 standard resolution spectroradiometer (PANalytical (formerly ASD Inc.), Longmont CO, USA). The spectral data were used to calculate the average reflectance of R (655-665nm) and FR light (725-735nm) and these were used to estimate the average R:FR of reflected light.

Number of leaves and angle (from the horizontal) of the oldest, healthiest leaf were measured weekly after seedling emergence. Leaf angle was measured using a protractor. Plants were harvested at 63 and 47 days after planting (DAP) in 2016 and 2017, respectively. At harvest, number of leaves, root length, root diameter, root fresh weight, root dry weight, total leaf area, shoot fresh weight, and shoot dry weight were measured. Root diameter and leaf area were measured using a digital caliper and leaf area meter (LI-3100C) (LI-COR Inc., Lincoln, Nebraska USA), respectively.

2.2 Data analysis

Nonlinear regression analysis was performed using the 'drc' package (v4.0-2) in the R statistical language (v 3.5.1) to quantify the effect of reflected light from neighboring species and soil surface on sugarbeet leaf number over time [25,26]. A three-parameter Weibull model was used (Equation 1), where Y is the number of sugarbeet 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 and, also have parameter estimates with meaningful biological interpretations [27]. The effect of reflected light from neighboring species on the number of sugarbeet true leaves at final harvest which corresponded with 63 and 47 d in 2016 and 2017, respectively was estimated from the model and 95% confidence intervals were calculated. Non-overlapping 95% confidence intervals were used as a conservative estimate of statistical difference between treatments [28].

$$Y = d * -\exp(b * (\log(x) - e)) \qquad [1]$$

A repeated measures analysis with a Satterthwaite denominator degree of freedom approximation to account for correlated errors was performed on sugarbeet leaf angle using the lme4 package [29]. For leaf angle, Tukey-adjusted pairwise treatment comparisons were performed using the 'emmeans' package [30]. Analysis of variance was performed on reflectance and harvest data (total leaf area, root length, root diameter, shoot dry weight, and root dry weight). Treatments differences were compared at alpha of 0.05 using Fisher's protected LSD.

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3. Results and Discussion

3.1 Light reflectance from plant canopies

The spectral signature of neighboring species and the bare soil showed that plant species reflected less than 20% of incoming R light and about 36 to 56% of incoming FR light (Figure 2). It is because photosynthetic pigments absorb more in the R region than the FR region of in-coming solar radiation [31].

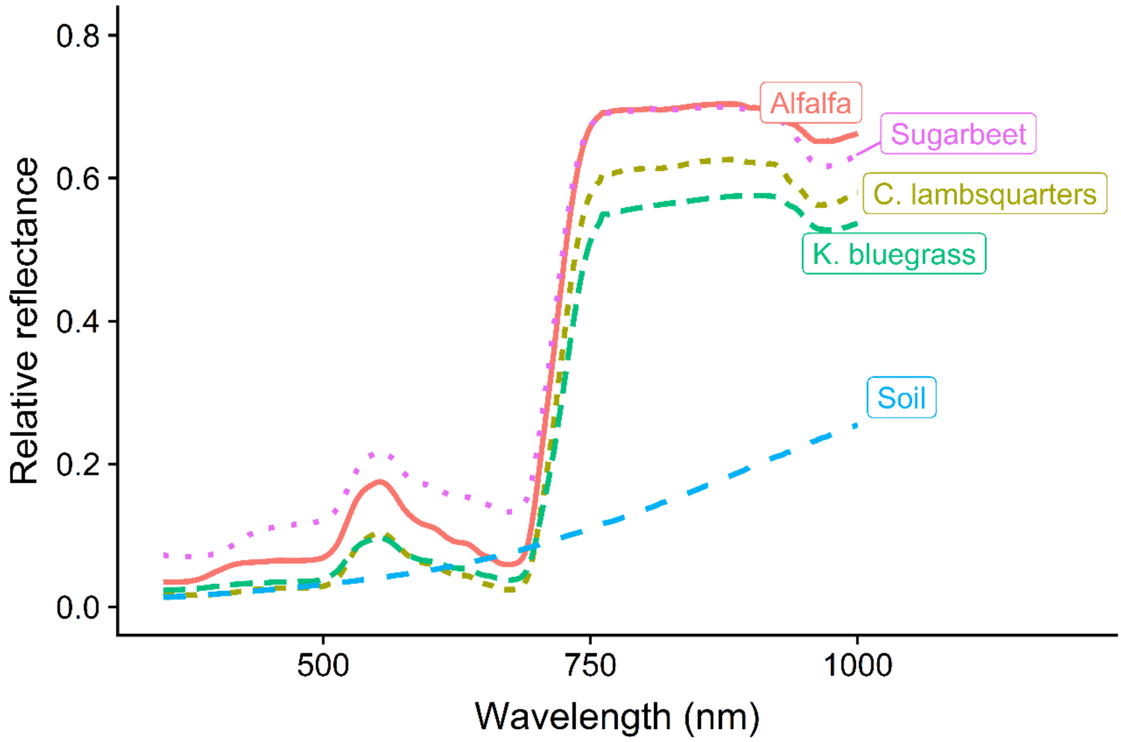

Figure 2. Reflectance spectra of alfalfa, sugarbeet, common lambsquarters, Kentucky bluegrass, and soil in the study (n=10 for each species).

The high levels of FR light reflected from the leaf surfaces explains the reduction in R:FR ratio in crowded plant communities [32,33]. Reflected R and FR light from maize (Zea mays L.) leave surface was reported to be approximately 5% and 40%, respectively [34]. There were differences in the relative amounts of R and FR light reflected by the plant species (Table 1). This resulted in differences ($P<0.0001$) in R:FR (Table 1). This might be due to differences in the greenness (chlorophyll concentration) and leaf surface brightness of the plant species. For example, visual observation showed that alfalfa and sugarbeet leaves were deep green in color compared to pale green color of common lambsquarters. The R:FR of plant species ranged from 0.06 (common lambsquarters) to 0.24 (sugarbeet) (Figure 2). This was within the range of 0.05-1.15 reported by [35].

Table 1 Relative reflectance of red and far-red light and red to far-red light ratio of neighboring species and bare soil surface in 2016, Laramie WY

Neighbor	Relative reflectance		
	Red (655-665nm)	Far-red (725-735nm)	Red to far-red
Alfalfa	0.07b†	0.54a	0.12c
Common lambsquarters	0.03d	0.43b	0.06d
Kentucky bluegrass	0.04c	0.36c	0.12c
Sugarbeet	0.14a	0.56a	0.24b
Soil	0.07b	0.10d	0.70a
P-value	<0.0001	<0.0001	<0.0001

†within column, means followed by same letters are not significantly different at the 0.05 probability level.

The soil surface had the greatest R:FR (0.7; Table 1). The R:FR of gray-white and brick-red soil surfaces were reported to be 1.0 and 1.18, respectively [34]. The lesser ratio obtained in this study was due to the potting media used. The potting media was mostly peat which has a dark brown to black color. Thus, most of the incoming radiation was absorbed by the media. Studies on light quality have shown that phytochrome photoequilibrium (the ratio of FR absorbing phytochrome to the sum of R and FR absorbing phytochrome) of daylight is about 0.81 [36] and stem extension was observed at phytochrome photoequilibrium of 0.63 (R:FR ~ 0.66) [37]. Although the results from Sager, Smith, Edwards and Cyr [36] and Craig and Runkle [37] were based on photosynthetic photon flux rather than the relative reflectance reported in this study, their results suggest that plants responded to marginal reductions in light quality.

3.2 Sugarbeet leaf angle

There was no time by treatment interaction effect on leaf angle in both 2016 ($P= 0.21$) and 2017 ($P = 0.15$). However, sugarbeet leaf angle was different in the presence of neighboring species in both 2016 and 2017 ($P < 0.001$). Sugarbeet grown with neighbors had more upright leaf angles (Figure 3). This modified morphology was initiated as early as 21 DAP in 2016 and 15 DAP in 2017 (data not presented). Leaf angle was lower in the soil treatment in both years (Figure 3). This shows that sugarbeet responded to reduced R:FR ratio and not necessarily species identity. Contrary to our results, Crepy and Casal [17] observed that Arabidopsis thaliana reorient leaves more horizontally when grown with kin than when grown with non-kin. They elucidated that the response involved the perception of R:FR and blue light. Mullen, et al. [38] reported that rosette leaves of A. thaliana were more vertically oriented when exposed to low light levels or shaded by neighboring leaves. However, leaves reorient horizontally when returned to white light. Reduced R:FR also increased leaf angle in tobacco [39]. Ethylene, a gaseous phytohormone essential in shade avoidance responses [40] increased leaf angle in A. thaliana [41].

Sugarbeet is rosette-forming in the first season of growth. Thus, the steeper leaf angles might be an adaptation for efficient light interception.

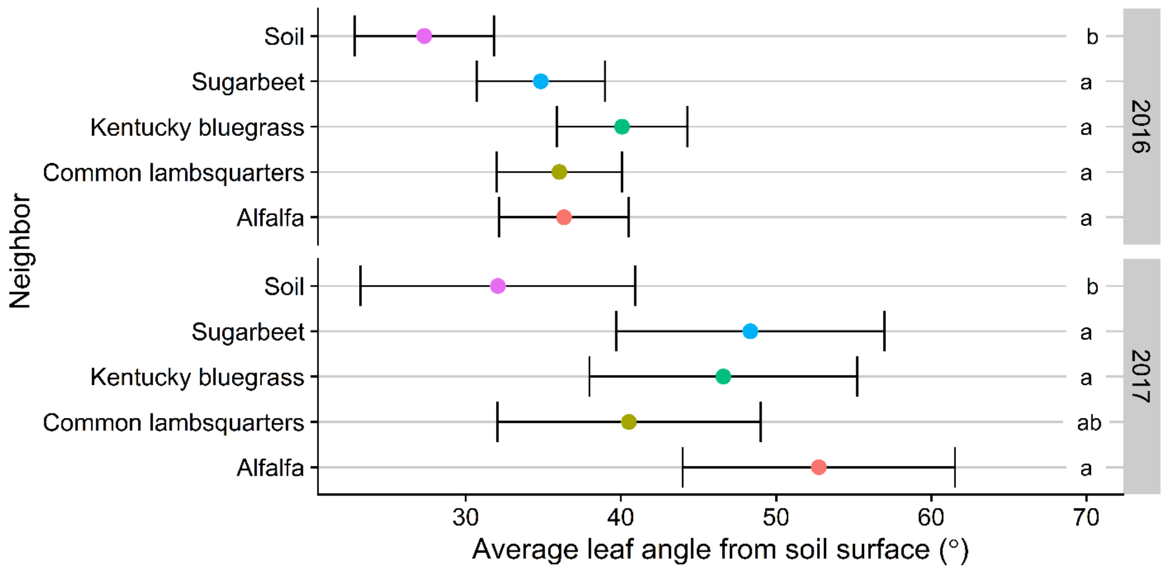

Figure 3. Effect of reflected far-red light from neighboring species on sugarbeet leaf angle (from the horizontal) in 2016 and 2017, Laramie WY. Within years, estimated marginal means followed by the same letter are not significantly different according to Tukey-adjusted pairwise comparisons (alpha = 0.05). Bars indicate 95% confidence interval.

At any given radiation stream, leaf angle (to the horizontal) determines the flux of solar radiation per unit leaf area [42,43]. However, the relationship between leaf angle and light interception is largely influenced by solar inclination. At low sun angles such as in the morning and late afternoon, steeper leaf angles increased solar radiation interception [43,44]. For example, light interception increased with increasing leaf angle (leaf angles between 25 to 75° to the horizontal) at 15° and 30°solar inclination [43]. Based on the findings by Falster and Westoby [43], it is estimated that with an average sugarbeet leaf angle of about 30° in the bare soil treatment and about 50° in the sugarbeet (kin) treatments in 2017 (Figure 3), direct light interception could be reduced by 12% and 22% at solar angles of 45°and 60°, respectively. However, at the canopy level, steeper leaf angles may reduce mutual shading and thus, maximize light interception [38]. Robson, McCormac, Irvine and Smith [20] stated that increased allocation of photosynthates for rapid stem expansion in dense crop stands is agriculturally wasteful. Allocation of assimilates to petioles and steeper leaf orientation might be important adaptation strategy in sugarbeet, because of the rosette growth and horizontal leaf architecture which makes sugarbeet leaves more prone to mutual shading. Thus, vertical leaf angles will be important when sugarbeet is planted at high densities.

3.3 Sugarbeet leaf number

The number of sugarbeet leaves was reduced by reflected FR light from neighoring species in both years of the study (Figure 4). Sugarbeet leaf appearance was delayed by the presence of neighboring species in both years such that at final harvest, there were 2 to 4 leaves in the sugarbeet surrounded by bare soil compared to sugarbeet surrounded by neighboring species (Figure 5; Table 2). Reflected FR from weeds was reported to have increased allocation to stem extension and reduced the number of visible leaf tips in maize [6,22,45]. Thus, the modified morphology (hyponasty) possibly resulting from an increased allocation to petiole growth might explain the reduced number of leaves observed in this study.

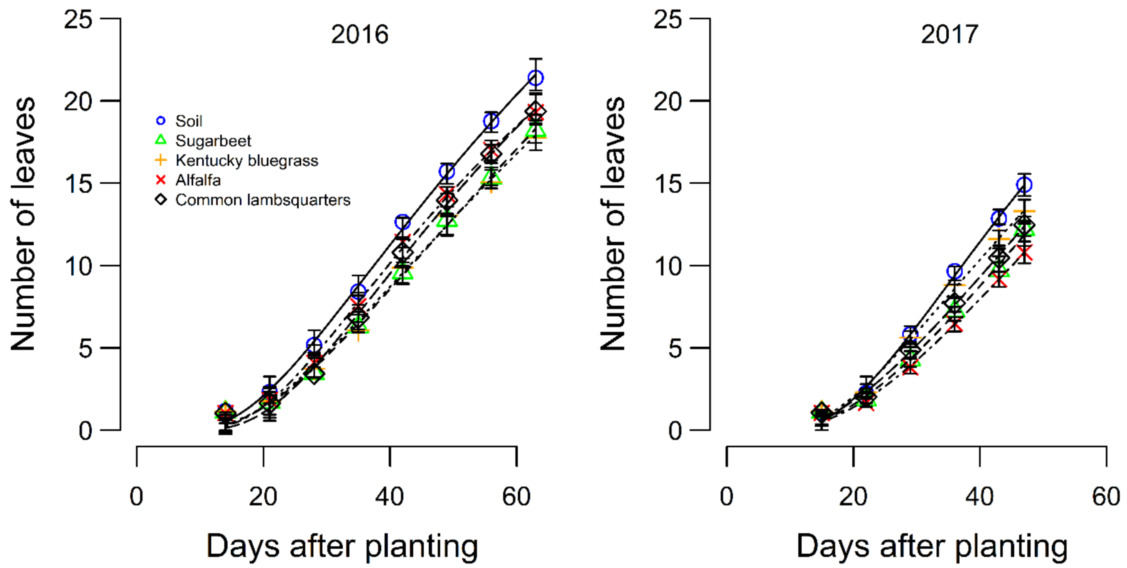

Figure 4. Effect of reflected far-red light from alfalfa, common lambsquarters, Kentucky bluegrass, sugarbeet, and bare soil on sugarbeet leaf number in 2016 and 2017, Laramie WY. Bars indicate 95% confidence interval.

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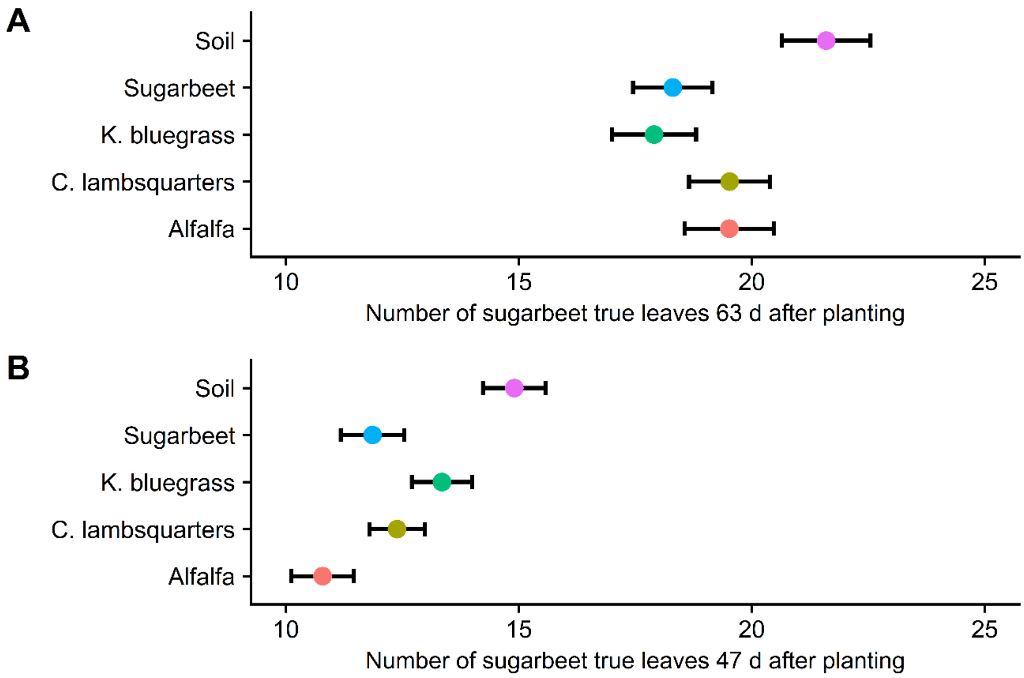

Figure 5. Effect of reflected far-red light from alfalfa, common lambsquarters, Kentucky bluegrass, sugarbeet, and bare soil on sugarbeet leaf number at 63 days in 2016 (A) and 43 days in 2017 (B), Laramie WY. Bars indicate 95% confidence interval, and non-overlapping confidence intervals were used as a conservative estimate of statistical difference between among [28]

Table 2. Parameter estimates describing sugarbeet leaf number following the three-parameter Weibull model for 2016 and 2017 experiments, Laramie WY.

	Parameter estimate (SE)†		
	b	*d*	*e*
Neighbor		**2016**	
Alfalfa	-1.1 (0.3)	51 (20)	61 (21)
Sugarbeet	-0.79 (0.3)	108 (88)	130 (109)
Common lambsquarters	-1.2 (0.3)	54 (23)	64 (22)
Kentucky bluegrass	-0.85 (0.4)	82 (76)	104 (96)
Soil	-0.90 (0.3)	78 (40)	83 (43)
		2017	
Alfalfa	-0.7 (0.2)	155 (123)	204 (160)
Sugarbeet	-0.64 (0.2)	188 (159)	228 (196)
Common lambsquarters	-0.7 (0.2)	140 (117)	171 (145)
Kentucky bluegrass	-0.90 (0.3)	68 (52)	81 (57)
Soil	-1.0 (0.4)	65 (50)	68 (44)

† Y = d * -exp(b * (log(x) - e)). Parameter estimates are described in text preceding Equation (1).

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3.4 Sugarbeet shoot and root growth

The presence of neighboring species reduced sugarbeet root diameter, leaf area, and shoot dry weight in 2016 (Table 3). However, sugarbeet root dry weight, root length, and shoot to root dry weight ratio were not affected by treatments. This was likely due to the late harvest in 2016 (63 d) that resulted in root-bound conditions. This is because sugarbeet in the bare soil treatment generally grew the fastest. Thus, a root bound condition early in the season would likely stall growth in the control treatment while other treatments have enough space for increased root growth. On the contrary, only root length and shoot to root dry weight ratio were not affected by neighboring species presence in 2017 (Table 3).

Table 3. Effect of reflected far-red light from neighboring species on sugarbeet growth at 63 days after planting (DAP) in 2016 and 47 DAP in 2017, Laramie WY

Neighbor	Leaf area	Root length	Root diameter	Shoot biomass	Root biomass	Shoot to root ratio
	cm^2	-----------cm------------		-------g $plant^{-1}$---------		
			2016			
Alfalfa	867±61b	24.6±3.1	3.5±0.2b†	12.1±1.1b	12.8±1.7	1.0±0.1
Sugarbeet	721±63b	32.8±4.4	3.0±0.3b	10.2±1.1b	10.0±2.7	1.6±0.5
Common	872±83b	31.8±3.1	3.7±0.3b	11.9±1.4b	13.2±2.8	1.2±0.2
Kentucky	790±54b	30.1±2.5	3.5±0.3b	10.4±0.9b	12.5±2.8	1.1±0.1
Soil	1139±95a	28.6±4.3	4.6±0.5a	16.4±1.4a	20.3±3.4	1.3±0.5
P-value	0.0047	0.5519	0.0268	0.008	0.1571	0.6617
			2017			
Alfalfa	433±60b	19.1±2.5	1.6±0.2b	3.8±0.7c	1.1±0.4b	4.2±0.7
Sugarbeet	550±58b	21.0±1.8	1.7±0.2b	5.4±0.7bc	1.4±0.4b	4.1±0.7
Common	523±58b	16.3±2.0	2.0±0.2b	4.8±0.7c	2.0±0.4b	3.1±0.5
Kentucky	813±94a	15.5±2.1	2.8±0.3a	8.3±1.3ab	4.2±1.0a	2.4±0.3
Soil	822±81a	20.0±2.5	2.8±0.3a	8.9±1.1a	3.8±0.7a	2.8±0.5
P-value	0.001	0.3626	0.0009	0.002	0.006	0.07

†within column and for each year, means followed by the same letters are not significantly different at the 0.05 probability level. ± indicate standard error of the mean.

Shade avoidance was reported to have affected sugarbeet growth and development [9]. Schambow, Adjesiwor, Lorent and Kniss [9] demonstrated that in the absence of resource competition, reflected FR light from Kentucky bluegrass canopies reduced sugarbeet leaf biomass, total leaf area, and root fresh weight by 30, 63, and 70%, respectively, when plants were harvested 90 DAP. Studies have also demonstrated that reflected FR light reduced leaf area and leaf biomass in maize [6,22], root and total biomass in maize [45]; leaf area, leaf, root, and total biomass in soybean [8]. The reduced sugarbeet leaf area and shoot dry weight (Table 3) was due to fewer leaves (Figure 4 & 5). Since there was no below-ground resource competition, differences in root length due to treatments was not expected. However, root diameter was expected to be more correlated with root weight. Thus, reduced allocation to roots due to reflected FR light from neighboring species reduced root diameter in both years (Table 3). In both years and for response variables where differences were observed, sugarbeet growth was greater when surrounded by soil than when surrounded by sugarbeet. These observations suggest that sugarbeet could not discriminate reflected FR light of kin from that of non-kin and this answered our research question. Sugarbeet responded to reduced light quality rather than absolute reductions in light quality. Previous studies have shown that Sorghum vulgare [46], Cycas micronesica [15], Cakile edentula [47], Ambrosia artemisiifolia [48] and Trifolium repens [24] were able to discriminate between kin and non-kin. However, there were root interactions in those studies, suggesting that direct root interaction may be required for kin recognition in some plants. This is because root exudates mediate neighbor recognition in most plants [49]. Aside from root interactions, volatile compound signals may also be involved in kin recognition and this has been found in Artemisia tridentata [50]. Thus, the lack of kin recognition observed in this study could be due to either the absence of root interaction or volatiles. Although results from this study suggest that reflected FR light from neighboring sugarbeets might affect growth, development, and yield of sugarbeet, this would largely depend on plant spacing and planting density. Thus, at low planting densities, it is likely that the effect of reflected light on sugarbeet growth might be minimal until canopy closure. It is concluded that sugarbeet could not differentiate reflected light quality of kin from that of non-kin.

Author Contributions: Conceptualization, A.TA. and A.R.K; methodology, A.TA. and A.R.K; software, A.T.A; validation, A.R.K.; formal analysis, A.T.A.; investigation, A.TA. and A.R.K; resources, A.R.K.; data curation, A.T.A.; writing—original draft preparation, A.T.A.; writing—review and editing, A.TA. and A.R.K.; visualization, A.T.A.; supervision, A.R.K.; project administration, A.R.K.; funding acquisition, A.R.K. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

References

1. Depuydt, S. Arguments for and against self and non-self root recognition in plants. *Frontiers in Plant Science* **2014**, *5*, 1-7, doi:ARTN 61410.3389/fpls.2014.00614.
2. Biedrzycki, M.L.; Bais, H.P. Kin recognition in plants: a mysterious behaviour unsolved. *Journal of Experimental Botany* **2010**, *61*, 4123-4128, doi:10.1093/jxb/erq250.
3. Roig-Villanova, I.; Martinez-Garcia, J.F. Plant Responses to Vegetation Proximity: A Whole Life Avoiding Shade. *Frontiers in Plant Science* **2016**, *7*, doi:ARTN 23610.3389/fpls.2016.00236.
4. Smith, H. The Ecological Functions of the Phytochrome Family - Clues to a Transgenic Program of Crop Improvement. *Photochemistry and Photobiology* **1992**, *56*, 815-822, doi:DOI 10.1111/j.1751-1097.1992.tb02238.x.
5. McKenzie-Gopsill, A.G.; Lukens, L.; Lee, E.; Swanton, C.J. Does the presence of neighbouring weeds alter the expression of adaptive plasticity to subsequent drought stress in soybean? *Field Crops Research* **2016**, *192*, 144-153, doi:10.1016/j.fcr.2016.04.029.
6. Page, E.R.; Tollenaar, M.; Lee, E.A.; Lukens, L.; Swanton, C.J. Shade avoidance: an integral component of crop-weed competition. *Weed Research* **2010**, *50*, 281-288, doi:10.1111/j.1365-3180.2010.00781.x.
7. Rajcan, I.; Chandler, K.J.; Swanton, C.J. Red-far-red ratio of reflected light: a hypothesis of why early-season weed control is important in corn. *Weed Sci* **2004**, *52*, 774-778, doi:Doi 10.1614/Ws-03-158r.
8. Green-Tracewicz, E.; Page, E.R.; Swanton, C.J. Shade Avoidance in Soybean Reduces Branching and Increases Plant-to-Plant Variability in Biomass and Yield Per Plant. *Weed Sci* **2011**, *59*, 43-49, doi:10.1614/ws-d-10-00081.1.
9. Schambow, T.J.; Adjesiwor, A.T.; Lorent, L.; Kniss, A.R. Shade avoidance cues reduce Beta vulgaris growth. *Weed Sci* **2019**, *67*, 311-317, doi:10.1017/wsc.2019.2.
10. Liu, J.G.; Mahoney, K.J.; Sikkema, P.H.; Swanton, C.J. The importance of light quality in crop-weed competition. *Weed Research* **2009**, *49*, 217-224, doi:10.1111/j.1365-3180.2008.00687.x.
11. Mehlis, M.; Bakker, T.C.; Frommen, J.G. Smells like sib spirit: kin recognition in three-spined sticklebacks (Gasterosteus aculeatus) is mediated by olfactory cues. *Animal Cognition* **2008**, *11*, 643-650.
12. Dudley, S.A.; Murphy, G.P.; File, A.L. Kin recognition and competition in plants. *Functional Ecology* **2013**, *27*, 898-906, doi:10.1111/1365-2435.12121.
13. Abakumova, M.; Zobel, K.; Lepik, A.; Semchenko, M. Plasticity in plant functional traits is shaped by variability in neighbourhood species composition. *New Phytologist* **2016**, *211*, 455-463, doi:10.1111/nph.13935.

14. Bhatt, M.V.; Khandelwal, A.; Dudley, S.A. Kin recognition, not competitive interactions, predicts root allocation in young Cakile edentula seedling pairs. *New Phytologist* **2011**, *189*, 1135-1142, doi:10.1111/j.1469-8137.2010.03548.x.
15. Marler, T.E.; Dongol, N.; Cruz, G.N. Plastic responses mediated by identity recognition in below-ground competition in Cycas micronesica KD Hill. *Tropical Conservation Science* **2016**, *9*, 648-657.
16. Karban, R.; Shiojiri, K.; Ishizaki, S.; Wetzel, W.C.; Evans, R.Y. Kin recognition affects plant communication and defence. *Proceedings of the Royal Society B-Biological Sciences* **2013**, *280*, doi:ARTN 2012306210.1098/rspb.2012.3062.
17. Crepy, M.A.; Casal, J.J. Photoreceptor-mediated kin recognition in plants. *New Phytologist* **2015**, *205*, 329-338, doi:10.1111/nph.13040.
18. Crepy, M.A.; Casal, J.J. Kin recognition by self-referent phenotype matching in plants. *New Phytologist* **2016**, *209*, 15-16, doi:10.1111/nph.13638.
19. de Wit, M.; Kegge, W.; Evers, J.B.; Vergeer-van Eijk, M.H.; Gankema, P.; Voesenek, L.A.; Pierik, R. Plant neighbor detection through touching leaf tips precedes phytochrome signals. *Proceedings of the National Academy of Sciences* **2012**, *109*, 14705-14710.
20. Robson, P.R.H.; McCormac, A.C.; Irvine, A.S.; Smith, H. Genetic engineering of harvest index in tobacco through overexpression of a phytochrome gene. *Nature Biotechnology* **1996**, *14*, 995-998, doi:DOI 10.1038/nbt0896-995.
21. Page, E.R.; Cerrudo, D.; Westra, P.; Loux, M.; Smith, K.; Foresman, C.; Wright, H.; Swanton, C.J. Why Early Season Weed Control Is Important in Maize. *Weed Sci* **2012**, *60*, 423-430, doi:10.1614/ws-d-11-00183.1.
22. Page, E.R.; Tollenaar, M.; Lee, E.A.; Lukens, L.; Swanton, C.J. Does the shade avoidance response contribute to the critical period for weed control in maize (Zea mays)? *Weed Research* **2009**, *49*, 563-571, doi:10.1111/j.1365-3180.2009.00735.x.
23. Wang, H.; Wu, G.X.; Zhao, B.B.; Wang, B.B.; Lang, Z.H.; Zhang, C.Y.; Wang, H.Y. Regulatory modules controlling early shade avoidance response in maize seedlings. *Bmc Genomics* **2016**, *17*, doi:ARTN 26910.1186/s12864-016-2593-6.
24. Lepik, A.; Abakumova, M.; Zobel, K.; Semchenko, M. Kin recognition is density-dependent and uncommon among temperate grassland plants. *Functional Ecology* **2012**, *26*, 1214-1220, doi:10.1111/j.1365-2435.2012.02037.x.
25. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Consulting. Vienna. Availabe online: Available: http://www.R-project.org/ (accessed on 20th August, 2020).
26. Ritz, C.; Baty, F.; Streibig, J.C.; Gerhard, D. Dose-response analysis using R. *Plos One* **2015**, *10*, e0146021.
27. Shafii, B.; Price, W.J.; Swensen, J.B.; Murray, G.A. Nonlinear estimation of growth curve models for germination data analysis. **1991**.
28. Austin, P.C.; Hux, J.E. A brief note on overlapping confidence intervals. *Journal of vascular surgery* **2002**, *36*, 194-195.

29. Bates, D.; Mächler, M.; Bolker, B.; Walker, S. Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv:1406.5823* **2015**.
30. Lenth, R. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.3.4. https://CRAN.R-project.org/package=emmeans. **2019**.
31. Martinez-Garcia, J.F.; Galstyan, A.; Salla-Martret, M.; Cifuentes-Esquivel, N.; Gallemi, M.; Bou-Torrent, J. Regulatory Components of Shade Avoidance Syndrome. *Advances in Botanical Research, Vol 53* **2010**, *53*, 65-116, doi:10.1016/S0065-2296(10)53003-9.
32. Casal, J.J. Photoreceptor signaling networks in plant responses to shade. *Annu Rev Plant Biol* **2013**, *64*, 403-427, doi:10.1146/annurev-arplant-050312-120221.
33. Mizuno, T.; Oka, H.; Yoshimura, F.; Ishida, K.; Yamashino, T. Insight into the mechanism of end-of-day far-red light (EODFR)-induced shade avoidance responses in Arabidopsis thaliana. *Bioscience Biotechnology and Biochemistry* **2015**, *79*, 1987-1994, doi:10.1080/09168451.2015.1065171.
34. Kasperbauer, M.; Karlen, D. Plant spacing and reflected far-red light effects on phytochrome-regulated photosynthate allocation in corn seedlings. *Crop Sci* **1994**, *34*, 1564-1569.
35. Neff, M.M.; Fankhauser, C.; Chory, J. Light: an indicator of time and place. *Genes & Development* **2000**, *14*, 257-271.
36. Sager, J.; Smith, W.; Edwards, J.; Cyr, K. Photosynthetic efficiency and phytochrome photoequilibria determination using spectral data. *Transactions of the ASAE* **1988**, *31*, 1882-1889.
37. Craig, D.S.; Runkle, E.S. A moderate to high red to far-red light ratio from light-emitting diodes controls flowering of short-day plants. *Journal of the American Society for Horticultural Science* **2013**, *138*, 167-172.
38. Mullen, J.L.; Weinig, C.; Hangarter, R.P. Shade avoidance and the regulation of leaf inclination in Arabidopsis. *Plant, Cell & Environment* **2006**, *29*, 1099-1106.
39. Pierik, R.; Cuppens, M.L.; Voesenek, L.A.; Visser, E.J. Interactions between ethylene and gibberellins in phytochrome-mediated shade avoidance responses in tobacco. *Plant Physiology* **2004**, *136*, 2928-2936.
40. Pierik, R.; Visser, E.J.W.; De Kroon, H.; Voesenek, L.A.C.J. Ethylene is required in tobacco to successfully compete with proximate neighbours. *Plant Cell and Environment* **2003**, *26*, 1229-1234, doi:DOI 10.1046/j.1365-3040.2003.01045.x.
41. Millenaar, F.F.; Cox, M.C.; van Berkel, Y.E.d.J.; Welschen, R.A.; Pierik, R.; Voesenek, L.A.; Peeters, A.J. Ethylene-induced differential growth of petioles in Arabidopsis. Analyzing natural variation, response kinetics, and regulation. *Plant Physiology* **2005**, *137*, 998-1008.
42. Niinemets, Ü.; Cescatti, A.; Christian, R. Constraints on light interception efficiency due to shoot architecture in broad-leaved Nothofagus species. *Tree Physiology* **2004**, *24*, 617-630.
43. Falster, D.S.; Westoby, M. Leaf size and angle vary widely across species: what consequences for light interception? *New Phytol* **2003**, *158*, 509-525.

44. James, S.A.; Bell, D.T. Leaf orientation, light interception and stomatal conductance of Eucalyptus globulus ssp. globulus leaves. *Tree Physiology* **2000**, *20*, 815-823.
45. Page, E.R.; Liu, W.D.; Cerrudo, D.; Lee, E.A.; Swanton, C.J. Shade Avoidance Influences Stress Tolerance in Maize. *Weed Sci* **2011**, *59*, 326-334, doi:10.1614/Ws-D-10-00159.1.
46. Zhang, L.; Liu, Q.Y.; Tian, Y.Q.; Xu, X.L.; Ouyang, H. Kin selection or resource partitioning for growing with siblings: implications from measurements of nitrogen uptake. *Plant and Soil* **2016**, *398*, 79-86, doi:10.1007/s11104-015-2641-z.
47. Dudley, S.A.; File, A.L. Kin recognition in an annual plant. *Biology Letters* **2007**, *3*, 435-438, doi:10.1098/rsbl.2007.0232.
48. File, A.L.; Klironomos, J.; Maherali, H.; Dudley, S.A. Plant Kin Recognition Enhances Abundance of Symbiotic Microbial Partner. *Plos One* **2012**, *7*, doi:ARTN e4564810.1371/journal.pone.0045648.
49. Semchenko, M.; Saar, S.; Lepik, A. Plant root exudates mediate neighbour recognition and trigger complex behavioural changes. *New Phytologist* **2014**, *204*, 631-637, doi:10.1111/nph.12930.
50. Karban, R.; Wetzel, W.C.; Shiojiri, K.; Ishizaki, S.; Ramirez, S.R.; Blande, J.D. Deciphering the language of plant communication: volatile chemotypes of sagebrush. *New Phytologist* **2014**, *204*, 380-385, doi:10.1111/nph.12887.