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Relative contribution of shade avoidance and resource competition to early-season sugar beet yield loss due to weeds

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Research Article

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Abstract

Shade avoidance alters the way plants grow, usually causing them to grow taller at the expense of placing resources into leaves, roots, seeds, and other harvestable materials. Sugar beet (*Beta vulgaris* L.) is a rosette-forming biennial species that has limited capacity to grow tall in the first year of growth. In the context of crop–weed competition, it is mostly unknown to what extent shade avoidance reduces yield in sugar beet relative to other effects like resource competition. To determine the extent of yield loss due to shade avoidance in a field-relevant situation, sugar beets were grown alongside Kentucky bluegrass (*Poa pratensis* L.) sod in a field study. Roots were separated with a steel root barrier placed into the ground between the grass and beets. Four treatments included a weed-free control (no root barrier or grass), a root barrier control (with root barrier but no grass), shade avoidance (with root barrier and grass), and full competition (with grass but no root barrier). The presence versus absence of grass was the primary driver of effects on measured sugar beet growth and yield parameters, regardless of whether a root barrier was present. Leaf number and root length were also impacted by the presence of the root barrier. These results suggest that shade avoidance is at least as important as root interactions and resource depletion in the context of early-season sugar beet yield loss due to weeds.

Introduction

Plants interfere with each other on a number of levels, both in competition for limited resources and through resource-independent interactions. The resource-independent responses include allelopathy, shade avoidance, and interference of symbiotic relationships. Resource competition responses include the interception of photosynthetically active wavelengths of light (shading) and belowground competition for resources such as water and nutrients (Nagata et al. 2015; Rajcan and Swanton 2001). Resource competition can be defined as "the capture of essential resources from a common, finite pool by neighboring individuals" (Horvath et al. 2023, p. 567). For decades, it was assumed that depletion of resources required by the crop was the primary driver of crop yield loss due to weeds. However, mounting research has shown that the presence of weeds can reduce crop yields even when resources available for optimal crop growth never become limiting (Horvath et al. 2023).

Plants have the ability to perceive and respond to the presence of neighboring individuals in ways that may significantly affect growth and yield. Plants absorb red (R) light (660 nm), while reflecting and transmitting far-red (FR) light (730 nm). Exposure to a low ratio of R:FR light represents a major mechanism of how plants sense neighbors, along with depletion of blue wavelengths and sensing of green light reflection (Ballaré and Casal 2000; Meng et al. 2019; Wang et al. 2018). Volatile organic compounds such as ethylene and thigmotactic responses also play a role in the neighbor-sensing process (De Wit et al. 2012; Yang and Li 2017). Neighbor sensing elicits a photomorphogenic growth pattern in plants known as the "shade avoidance response," which has consequences for crop yield in agriculture (Adjesiwor et al. 2021; Green-Tracewicz et al. 2011; Rajcan and Swanton 2001; Schambow et al. 2019).

Symptoms of the shade avoidance response typically involve an investment in stem tissues, elongation growth patterns, reduced total biomass, decreased blade:petiole ratio, and reduced investment in fibrous roots (Farquharson 2010; Green-Tracewicz et al. 2011; Page et al. 2009; Schambow et al. 2019). Changes in plant growth due to shade avoidance represent an important mechanism of yield loss due to weeds in several crops harvested for seed grain. In soybean [*Glycine max* (L.) Merr.], seed yield was reduced 10% due to shade avoidance (Green-Tracewicz et al. 2011). For corn (*Zea mays* L.), the overall seed yield was not affected by shade avoidance, although the aboveground mass of the plants was clearly affected (Page et al. 2010, 2011). While overall seed mass per plant was not affected by shade avoidance, the kernel number was lower in plants experiencing shade avoidance, which indicates the overall fitness of the plant and possibly the yield potential are affected (Page et al. 2010). Canola (*Brassica napus* L.) given low R:FR through filters showed no change in grain yield in response to shade avoidance (Rondanini et al. 2014). Although shade avoidance does not reliably affect the final yield of plants grown for seed, the morphology of the plant is clearly affected by shade avoidance in nearly all cases. Shade avoidance affects branching in soybeans, the mass of stems, as well as the size of the leaves (Page et al. 2009, 2011). In corn, the height of the plant increased while the number of leaves decreased (Page et al. 2011). Because plant morphology is more reliably affected by shade avoidance than seed yield, shade avoidance may have greater consequences in root crops or forage species, which rely directly on the plant's biomass for yield and quality.

Sustainable crop and weed management will benefit from a greater understanding of the causes of crop yield loss from weeds. For example, if crop yield is being reduced mostly from nutrient or water depletion from weeds, then it may be possible to maintain yield potential simply by adding fertilizer or irrigation. However, if crop yield is reduced more by physiological changes arising from neighbor sensing of weeds, then those inputs would be wasted. Weed management in many crops relies on postemergence control of weeds; if the shade avoidance response triggered by emerged weeds is responsible for substantial crop yield loss, then optimizing yield may require more focus on preventative measures such as very early season weed removal.

In many crops, much remains unknown about the mechanisms of plant interference in the context of crop yield loss. Because roots are the primary economic portion of the sugar beet (*Beta vulgaris* L.) plant, it makes an interesting model species for sorting out these dynamics. Previous work has shown that shade avoidance responses due to nearby weeds, even in the absence of direct resource competition, may be responsible for between 20% and 70% yield loss due to weeds in sugar beet (Adjesiwor et al. 2021; Adjesiwor and Kniss 2020; Schambow et al. 2019). Previous experiments in sugar beet were performed using methods that did not allow for direct root interactions or resource depletion in order to ensure the observed responses were due to shade avoidance. It is important to confirm whether sugar beets respond to these cues similarly in more field-realistic situations and to begin teasing apart the relative contribution of shade avoidance compared with direct competition for resources. The objective of this field study was to determine the relative contribution of shade avoidance and resource competition to early-season sugar beet growth reduction and yield loss when grown under field conditions.

Materials and Methods

This field experiment was conducted at the University of Wyoming Laramie Research and Extension Center (41.3196°N, 105.5592°W, 2,212 m elevation) during the summer of 2020, and repeated in 2021. Soil at the site is Wycolo-Alcova complex (fine-loamy, mixed, superactive, frigid Ustic Calciargids). The experimental design was a randomized complete block design with two factors (grass and root barrier). Thirty-six sugar beet seeds ('W746NT') were planted per 122-cm row and were later thinned to 8 plants spaced 15 cm apart (Figure 1). Plants were irrigated using an overhead sprinkler throughout the experiments. For grass treatments, Kentucky bluegrass (*Poa pratensis* L.) sod sourced from local retailers was planted alongside the sugar beet rows (Figure 1). Grass was trimmed weekly to ensure the sugar beets were not directly shaded by grass. Hammer-in landscape metal edging of 122 cm in length and 20 cm in height (Edge Right, Lewis Bamboo, Oakman, AL, USA) was used as a root barrier to separate grass roots from sugar beet roots by pounding the edging into the soil alongside the sugar beet row.

A factorial arrangement of grass (presence or absence) and root barrier (presence or absence) treatments were used for a total of four weed-exposure treatments (Figure 1). A weed-free control had neither root barrier nor grass (B−/G−) and this reflects the way plants are grown in agricultural contexts where weeds have been adequately controlled. A root barrier control had root barrier but no grass (B+/G−), which was included to measure the potentially negative effect of growing sugar beets within rows bordered by the root barrier. The shade avoidance treatment had both root barrier and grass (B+/G+) to allow sugar beets to perceive aboveground shade avoidance cues from surrounding low-growing grass but prohibit direct interaction and resource depletion by the grass roots. The fourth treatment was the full competition treatment, which had grass but no root barrier (G+/B−), which most directly simulates sugar beets growing among low-growing weeds. At the end of the season, soil was removed around the sugar beet rows, and root systems were inspected to ensure no direct interaction occurred below the root barrier.

Sugar beets were harvested 67 d after planting (DAP) in 2020 and 60 DAP in 2021. During harvest, all plants were pulled from each plot, and leaves on each plant were separated and counted. Leaf area was measured using a LICOR LI-3100C (Li-Cor, Lincoln, NE, USA) within 72 h of harvest. Leaves not immediately processed were sealed in ziplock bags stored at 4 C in dark conditions until processing. Root length and diameter at the widest point were measured using rulers and digital calipers, respectively. Roots and leaves were then dried for 72 h at 60 C and weighed.

Linear mixed-effects models were used to quantify the effect of grass and root barrier (fixed effects) and study year (random effect) on all response variables. Where the ANOVA indicated significant treatment effects (alpha $\leq$ 0.05), estimated marginal means were separated with pairwise comparisons. Statistical analysis was performed in R v. 4.3.1 (R Core Team 2023) using the LME4, MULTCOMP, EMMEANS, and LMERTEST packages (Bates et al. 2015; Hothorn et al. 2008; Kuznetsova et al. 2017; Lenth 2023), and figures were created using the TIDYVERSE and COWPLOT packages (Wickham et al. 2019; Wilke 2020).

Results and Discussion

The grass by root barrier interaction effect was significant for the number of leaves at harvest (Table 1). The shade avoidance treatment (B+/G+) reduced sugar beet leaf number by 32%, while the full competition treatment (B−/G+) reduced leaf number by 53% compared with the weed-free control (Figure 2). The root barrier control treatment (B+/G−) did not significantly reduce sugar beet leaf numbers.

Leaf area and leaf biomass production were affected by the presence of grass, but not by the presence of the root barrier (Table 1). The presence of grass reduced sugar beet leaf area by 81% when averaged over barrier treatments (Figure 2). Sugar beet leaf biomass showed a similar trend, with the presence of grass reducing leaf biomass by 83% when averaged over root barrier treatments. In experiments performed in 22-L pails using corn as a model, leaf length was found to increase in older leaves (Page et al. 2011). Specific leaf area was found to be smaller in older leaves, but total leaf area was unchanged (Page et al. 2011).

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Table 1. Partial ANOVA table for the effect of root barrier and grass presence on sugar beet leaf and root parameters 60 to 67 d after planting in Laramie, WY, 2020–2021.

	Mean square *P-value*						
	Leaf number	Leaf area	Leaf biomass	Root length	Root diameter	Root biomass	Root: shoot
Fixed effects							
Grass	434	5,767,278	691	192	2,514	505	0.68
	<0.001	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*0.362*
Root barrier	16	15,664	1	15	77	0.04	1.2
	0.201	*0.740*	*0.872*	*0.128*	*0.342*	*0.967*	*0.227*
Grass × root barrier	49	345,547	37	86	152	31	0.78
	0.025	*0.123*	*0.110*	*<0.001*	*0.182*	*0.228*	*0.330*
Random effects variance							
Year	0	16,116	0	0	64.9	0	0.006
Residual	9.34	140,897	21.9	6.15	83.2	21.2	0.809

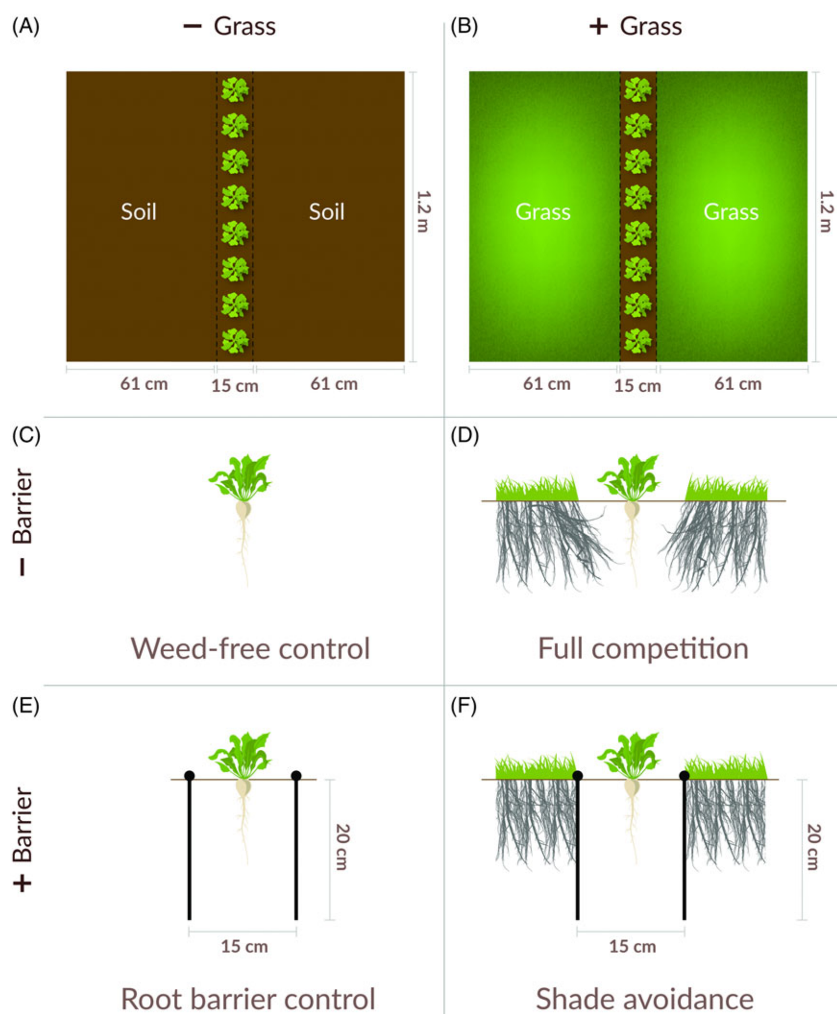

Figure 1. Diagram of the four treatments as placed in the field. Top view of the grass (A) and no-grass (B) treatments and cross sections of the weed-free control (C), full competition (D), root barrier control (E), and shade avoidance (F) treatments. Image created by Jessica Perry.

Soybean plants grown under low R:FR supplied by filters grew smaller, thinner leaves and had reduced overall leaf area (Wu et al. 2017). For both leaf area and leaf biomass, the root barrier had minimal effect in the presence of grass. This suggests that the aboveground light interactions explain a majority of the total interference effect during the first 2 mo of crop growth, with belowground interactions, including resource depletion by weeds, having a lesser impact. This finding is probably indicative of what would be found in commercial production fields, because annual weeds are likely to have relatively shallow root systems, as did our Kentucky bluegrass sod, during this early period of crop growth.

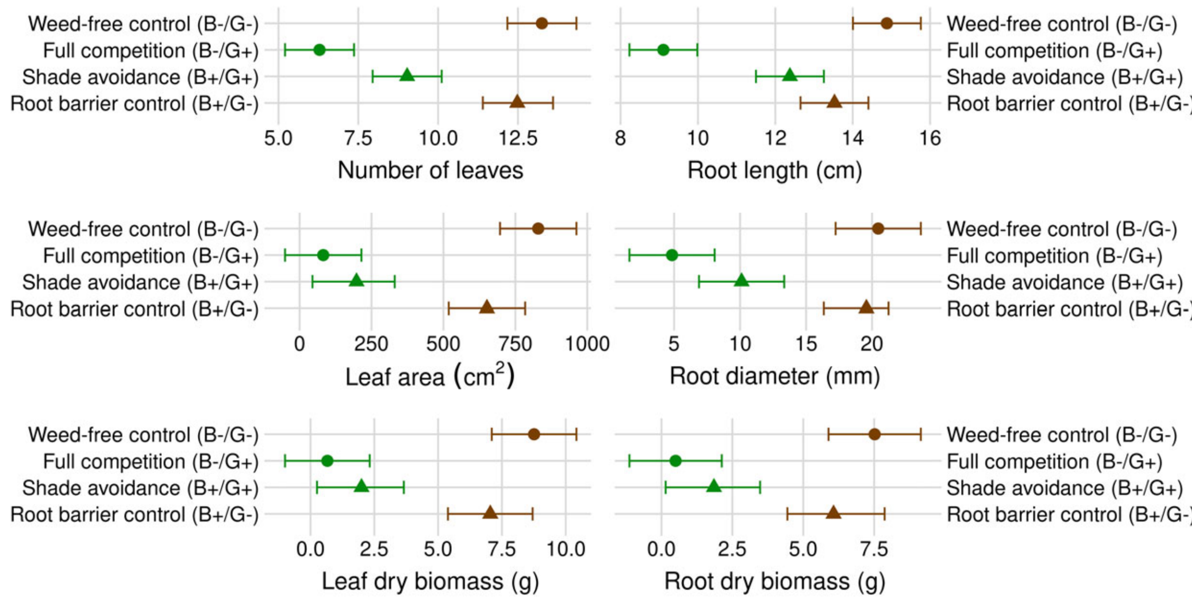

Figure 2. Leaf number per plant, leaf area, leaf biomass (left), taproot length, taproot diameter, and root biomass (right) harvested 60 to 67 d after planting as influenced by the presence of root barrier (B) or neighboring grass (G) in Laramie, WY, 2020 and 2021. Points represent the per-plant estimated marginal mean. Bars indicate the least significant difference; bars within a panel that extend horizontally beyond another treatment mean indicate the null hypothesis of no difference cannot be rejected based on a pairwise comparison (alpha = 0.05).

Sugar beet taproot length was affected by the interaction of grass and barrier presence (Table 1). The root barrier control treatment reduced sugar beet root length by 9% compared with the weed-free control (Figure 2). The shade avoidance treatment (B+/G−) reduced root length by 17% compared with the weed-free control, and the full competition treatment (B−/G+) reduced sugar beet root length by 39%. Sugar beet root diameter and root biomass were primarily affected by the presence of grass, and not by the presence of the root barrier or the interaction between these factors (Table 1). Compared with the weed-free or root barrier control treatments, the presence of grass reduced root diameter by 37% and root biomass by 17% (Figure 2). Root diameter and root biomass was slightly lower in the full competition treatment (B−/G+) compared with the shade avoidance treatment (B+/G+), but in neither case was the difference statistically significant ($P = 0.37$ and $P = 0.84$, respectively).

Previous researchers have suggested that shade avoidance must be considered in developing the critical period of weed control in crops (Green-Tracewicz et al. 2011; Page et al. 2009; Rajcan et al. 2004). Work by Adjesiwor et al. (2021) supports the importance of shade avoidance in sugar beet, showing that even in the absence of resource competition, shade avoidance cues present from sugar beet emergence until the two true-leaf stage reduced sugar beet root biomass by 32%. The current field study presented here has demonstrated that sugar beet yield loss observed in the first 2 mo after planting is more attributable to shade avoidance than to more traditionally recognized aspects of resource competition, like water or nutrient depletion. Shade avoidance responses are typically initiated before direct competition for light, water, and nutrients, and thus our findings here make intuitive sense. Even so, while we have known for decades that early-season weed control is important to protect sugar beet yield, the mechanism for this early-season impact of weeds on sugar beet yield has been largely unexamined.

The combined impact of shade avoidance and root interaction significantly impacted the number of sugar beet leaves and root length in the first 2 mo of growth, but all other measured response variables were primarily impacted by shade avoidance, with a substantially lesser effect of root interaction. The current field study substantiates results of previously performed large-pot studies that showed significant effects of shade avoidance on sugar beet yield potential (Adjesiwor et al. 2021; Adjesiwor and Kniss 2020; Schambow et al. 2019) and adds context, showing that the contribution of shade avoidance responses likely outweighs the impacts of resource depletion by weeds during the first 60 d of growth.

Substantial previous research on shade avoidance has characterized how plants adapt to the altered light environment caused by dense surrounding vegetation, and this work adds to that body of literature. With respect to its relevance to agronomic crops, most previous work has been done in crops harvested for seed, like corn and soybean. Because many aspects of plant morphology are reliably affected by shade avoidance, shade avoidance may have greater consequences in cropping systems that rely directly on the plant's root or leaf biomass for yield. For sugar beet, a biennial crop harvested as an annual for its root, our research here suggests shade avoidance is more impactful to early-season growth than belowground competition for resources. The current work shows results only for the first 60 to 67 d after planting (DAP). It is likely that the early-season effects reported here will predispose the sugar beets to greater impacts of resource competition later in the season. Reduced root biomass due to shade avoidance will reduce the crop's ability to compete for soil water or nutrients as those resources become limiting. The reduced leaf area and biomass will have similar detrimental impacts on the ability of the crop to gather light. Greater understanding of the *mechanism* by which weeds reduce crop yield may lead to improved weed management strategies over the long term (Rajcan and Swanton 2001). The differences between sugar beet and other crops reinforces that the impact of weeds on yield potential are crop specific. Continued research should be focused in this area to more fully explore the ways in which weeds impact important production systems.

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