The Effects of Light-Emitting Diode and Conventional Lighting on Sorghum Physiology and Sugarcane Aphid Interaction

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The effects of light-emitting diode and conventional lighting on sorghum physiology and sugarcane aphid interaction

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Abstract

Light-emitting diodes often are used to substitute and enhance fluorescent or incandescent light for plants that are grown in climate-controlled environments. These lights often are chosen over other light sources because of the light-emitting diodes' durability, long life, enhanced wavelength for specific plant species, lower energy costs, lower surface heat safety risk, and easier ability to incorporate into advanced climate control systems. However, previous studies have shown that characteristics of *Sorghum bicolor* (L.) Moench (Poaceae) are altered under light-emitting diodes. Therefore, we grew 4 cultivars of sorghum in growth chambers with either conventional or light-emitting diodes. Plants were infested with either the sugarcane aphid, *Melanaphis sacchari* (Zehntner) (Hemiptera: Aphididae) or were un-infested (control). Sorghum grown under light-emitting diodes was shorter and produced more leaves that were wider than those of plants grown under conventional lights. Two of the cultivars had lower photosynthetic rates and reduced stomatal conductance under light-emitting diodes. When exposed to sugarcane aphids, resistant cultivars tolerated aphid feeding with reduced damage under conventional lights but were similar to susceptible cultivars when grown under light-emitting diodes. Our results suggest that light-emitting diodes affect sorghum physiology and morphology, and also compromises resistance to herbivores. Our study provides further evidence that the physiological effects of different light spectra and interaction of plant defenses and herbivores need to be tested across a broad range of plant groups.

Key Words: plant resistance; grow lights; photosynthesis; Aphididae

Resumen

Los diodos emisores de luz a menudo se utilizan para sustituir y mejorar la luz fluorescente o incandescente para las plantas que se cultivan en entornos con clima controlado. Estas luces a menudo se eligen en lugar de otras fuentes de luz debido a la durabilidad de los diodos emisores de luz, su larga vida útil, su longitud de onda mejorada para especies específicas de plantas, sus costos de energía más bajos, su riesgo de seguridad contra el calor superficial más bajo y su capacidad más fácil de incorporarse a sistemas avanzados de control climático. Sin embargo, estudios previos han demostrado que las características de *Sorghum bicolor* (L.) Moench (Poaceae) se alteran bajo luces de diodos emisores de luz. Por lo tanto, cultivamos 4 cultivares de sorgo en cámaras de crecimiento con luces convencionales o con diodos emisores de luz. Las plantas estaban infestadas con el pulgón de la caña de azúcar, *Melanaphis sacchari* (Zehntner) (Hemiptera: Aphididae) o no estaban infestadas (control). El sorgo cultivado bajo luces de diodos emisores de luz era más corto y producía más hojas que eran más anchas que las de las plantas cultivadas bajo luces convencionales. Dos de los cultivares tenían tasas fotosintéticas más bajas y conductancia estomática reducida bajo luces de diodos emisores de luz. Cuando se expusieron a los áfidos de la caña de azúcar, los cultivares resistentes toleraron la alimentación de áfidos con daños reducidos bajo luces convencionales, pero fueron similares a los cultivares susceptibles cuando crecieron bajo iluminación con diodos emisores de luz. Nuestros resultados sugieren que las luces de diodos emisores de luz afectan la fisiología y morfología del sorgo y también comprometen la resistencia a los herbívoros. Nuestro estudio proporciona más evidencias de que los efectos fisiológicos de diferentes espectros de luz y su interacción con las defensas de las plantas y los herbívoros deben probarse en una amplia gama de grupos de plantas.

Palabras Claves: resistencia de las plantas; luces de crecimiento; fotosíntesis; Aphididae

Light is essential for plant growth and development, and can be provided to plants by natural sunlight or by other means such as incandescent, fluorescent, or light-emitting diodes. In horticulture, high-value plants can be grown under optimal environmental conditions, including altered light spectra and altered light cycles (Mukish et al. 2017). In addition, light sources that conserve energy, are longer lasting, and can be integrated easily into digital systems, such as those found in greenhouses and growth chambers, are in high demand.

Photosynthesis is dependent highly on light characteristics. Wavelengths, light duration, and light intensity all combine to affect plant growth and health. Light can also cause stress on plants. For example, when light intensity is high and plants face other abiotic stressors, plants can exceed the requirement for metabolic processes in carbon-fixing reactions where photosynthesis production decreases plant growth, slowing or stopping plant development (Miyake et al. 2009; Gu et al. 2017; Bayat et al. 2018). Previous studies have documented

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species-specific light stress (Hogewoning et al. 2010; Nanya et al. 2012; Cope & Bugbee 2013) among plants with C3 and C4 photosynthetic pathways.

Light-emitting diode technology has been at the forefront of horticulture and greenhouse production because of its improved photosynthetic delivery of specific light spectra and significantly reduced energy costs (Hogewoning et al. 2007; Massa et al. 2008; Trouwborst et al. 2010). Light-emitting diodes are the first artificial light source where the light-emitting spectrum is controlled mostly under the blue and red spectra (Morrow 2008), and unlike conventional lights have low surface operating temperatures.

Despite the increasing use of light-emitting diode technology, the potential effects of light-emitting diodes on plant characteristics have received relatively little attention. In general, light-emitting diodes have been shown to be capable of sustaining normal plant growth, although effects on chloroplasts and changes to leaf morphology have been noted (Darko et al. 2014). In some cases, high radiant exposure (fluence) generated by some light-emitting diodes triggers increases in secondary plant compounds and can influence the characteristics of plant stored nutrients (reviewed by Darko et al. 2014). More recently, Park (2018) examined plant response to different light intensities and found effects on plant growth and development characteristics for some, but not all tested plant species.

Some difference in response to light-emitting diodes appears to relate to plant photosynthetic systems. C3 plants generally have been found to perform well under light-emitting diodes. Studies of C3 plants have included tobacco (*Nicotiana tabacum* L. [Solanaceae]), spinach (*Spinacia oleracea* L. [Amaranthaceae]), radish (*Raphanus raphanistrum* L. [Brassicaceae]), lettuce (*Lactuca sativa* L. [Asteraceae]), and strawberry (*Fragaria* L. [Rosaceae]) (Brown et al 1995; Yorio et al. 2001; Nhut et al. 2003). In addition to successful growth characteristics, lettuce (*Lactuca*) grown under blue light-emitting diodes had higher antioxidant activity and enhanced seedling growth (Johkan et al. 2010; Darko et al. 2014).

Tobacco is a C3 plant that also has a C4 pathway and has shown positive reactions to light-emitting diodes (Jun et al. 2014). Light-emitting diodes promoted growth and reduced the membrane lipid peroxidation damage of the plant (Jun et al 2014). Similarly, when wheat, *Triticum aestivum* L. (Poaceae), a C4 plant, is grown under light-emitting diodes, it produces more tillers, biomass, yield, and increases photosynthetic activity (Casati et al. 1997; Monostori et al. 2018). In contrast, Limaje et al. (2019) found that sorghum, *Sorghum bicolor* (L.) Moench (Poaceae), had altered plant morphology and reduced biomass when grown under light-emitting diodes compared to the same cultivars of sorghum, grown under conventional light sources.

Sorghum is a C4 plant that is grown in semi-arid parts of the world where droughts are common. Sorghum is grown as food for human consumption, silage for livestock, the production of biofuel, and as a cover crop (Miron et al 2007; Bean et al. 2013; Anjali et al. 2017; Pino & Heinrichs 2017). Researchers and breeders often develop sorghum cultivars in greenhouses where agronomic and breeding experiments are conducted under controlled environmental conditions (Armstrong et al. 2015; Paudyal et al. 2019).

Although much research has been conducted to examine plant response to light-emitting diodes, less research has examined plant-insect interactions under light-emitting diodes. Rechner et al. (2016) examined cabbage aphids *Brevicoryne brassicae* (L.) and green peach aphids *Myzus persicae* (Sulzer) (both Hemiptera: Aphididae) grown on broccoli (*Brassica oleracea* var. *italica* L.; Brassicaceae) under light-emitting diodes. The specialist cabbage aphids had decreased performance while the generalist green peach aphid had increased performance (Rechner et al. 2016) under light-emitting diodes suggesting that the plant defenses were affected. Limaje et al. (2019) showed that interactions between sugarcane aphid, *Melanaphis sacchari* Zehntner (Hemiptera: Aphididae), and resistant and susceptible sorghum cultivars differed by lighting conditions with aphids exhibiting altered behaviors under light-emitting diodes. However, the light-emitting diodes used in the study by Limaje et al. is no longer manufactured and additional trials are warranted.

In this study, we examined the effects of standard 9-band light-emitting diodes on sorghum morphology and physiology, and characterized interactions between known susceptible and resistant cultivars and the sugarcane aphid. We also examined the plant's physiological responses to lighting and aphid feeding to gain insights into the reasons for different responses. Because plant response to herbivory is used as a method to identify plant resistance, gaining knowledge of the effects of experimental condition on the outcomes is critical to future studies.

Materials and Methods

APHID CULTURE

Sugarcane aphids were originally collected from Matagorda County, Texas, USA, in 2013 from infested grain sorghum. The colony is maintained as parthenogenic clones on susceptible 'TX-7000' sorghum seedlings at the USDA-ARS Laboratory in Stillwater, Oklahoma, USA. Susceptible seedlings are used to maintain sugarcane aphids in pots covered with sleeve cages in the greenhouse where the temperatures ranged between 21 and 31 °C. The clonal sugarcane aphids are transferred to fresh new susceptible seedlings every wk in the greenhouse to ensure continual supply of live colonies. The colony plants and aphids are grown under natural greenhouse light that is supplemented with 2 T-8 fluorescent lights. The supplemented lights are on timers so that the lights turn on at 6:00 AM Central Standard Time and turn off at 8:00 PM Central Standard Time (a 14:10 h [L:D] photoperiod).

SORGHUM ENTRIES AND CULTURE

All experiments were conducted between 4 Jun and 28 Jul 2020. Two sorghum varieties that are susceptible to sugarcane aphid, 'KS-585' and variety 'TX-7000,' and 2 that are resistant to sugarcane aphids, 'TX-2783' and 'DKS-37-07,' were used (Paudyal et al. 2019). All varieties were planted in Cone-tainers (model SC10; S7S Greenhouse Supply, Tangent, Oregon, USA). Each Cone-tainer™ was filled with a 3-layer system of different potting media from the bottom up: 120 g potting soil, 60 g fitting clay, and 30 g of sand. Each Cone-tainer™ was housed in an 8-cm diam Lexan sleeve (Tulsa Plastics, Tulsa, Oklahoma, USA) with a height of 45 cm, which was ventilated with organdy cloth. Both un-infested (control) and infested plants were planted and sleeved in the same way.

Initially, 2 seeds of each genotype were planted at a depth of 2 cm in the Cone-tainer™. The seedlings were grown under 2 T-8 fluorescent lighting (16:8 h [L:D]) at 25 ± 3 °C. One wk after planting the seedlings were thinned to 1 seedling per Cone-tainer™. One day after thinning, the plants were transferred from the greenhouse to growth chambers. All plants were fertilized with Miracle-Gro (Miracle-Gro, Mansville, Ohio, USA) Garden feeder at the recommended rate of 15 mL per 3.79 L.

GROWTH CHAMBERS

Four identical growth chambers (Percival Scientific, model E30B, Perry, Iowa, USA) that provide temperature, light, and humidity control were used in this study. Two of the growth chambers were maintained as originally fitted with 2 Philips (model 7866113, Philips Inc., Guadalajara, Jalisco, Mexico) fluorescent grow lights, and 2 clear 40-watt appliance lights (Sylvania, Wilmington, Massachusetts, USA). The other 2 chambers were fitted with 9-band 60-watt light-emitting diodes grow panels mounted in the top where the conventional lights were affixed originally. The light-emitting diodes had input voltage of approximately 85 to 265 volts. The power was 600 watts with a light-emitting diode configuration of 288 PCSX3W and 9 bands. The light intensity within the growth chambers lit by conventional lights and the light-emitting diode panels were measured with a LI-COR light meter (model LI-250, LI-COR, Lincoln, Nebraska, USA). The light-emitting diode spectra were measured with a Liconix Model 45PM (Downers Grove, Illinois, USA) spectrophotometer set to 100.

Fourteen days after planting, when plants were at the 4-leaf stage, the sorghum seedlings were infested with 10 adult sugarcane aphids per plant. All aphids were the same age when put on the plant. To ensure that all aphids were the same age, adult aphids from the main colony were put on extra plants of the 4 different genotypes and allowed to reproduce for 12 h. After 12 h, adult aphids were removed from each plant leaving only the nymphs. After the nymphs reached 7 d of age, they were transferred to the test genotypes in the growth chambers. Thus, all 10 aphids infested per plant were the same age, and been reproduced and grown on the sorghum genotype on which they were used to infest.

In total, there were 192 sorghum seedlings used in this study. There were 12 plants of each genotype tested in each of the 4 treatments: light-emitting diode grow lights with aphids, light-emitting diode grow lights with no aphids, conventional lights with aphids, and conventional lights with no aphids. Within each chamber, all plants were randomly placed using a random number generator. Plants were examined 15 d after infestation when susceptible plants (KS-585 and TX-7000) exposed to aphids were 90% dead. All aphids were removed before measurement of response variables.

PLANT-RESPONSE MEASUREMENTS

After physiological measures were obtained, plant height was measured from the soil line to the longest leaf tip. The number of true leaves was recorded and the maximum leaf width was measured at the widest point on the widest leaf on the plant.

All plants were evaluated using a damage rating scale of 1 to 9 (Webster et al. 1990; Burd et al. 2006). In the damage rating scale, 1 is a completely healthy plant with no necrotic tissue; 2 represents 1 to 5% chlorotic tissue; 3 represents 6 to 20%; 4 represents 21 to 35%; 5 represents 36 to 50%; 6 represents 51 to 65%; 7 represents 66 to 80%; 8 represents 81 to 95%; and 9 represents 96 to 100% chlorotic tissue or a dead plant.

To quantify chlorosis, a chlorophyll meter (model SPAD-502, Minolta Camera Co., Osaka, Japan) was used to measure chlorophyll content. The chlorophyll meter absorbs light at wavelengths between 430 and 750 nm and estimates chlorophyll content in the leaf (Wood et al. 1992). Three readings from different leaves were taken from each plant. A SPAD chlorophyll index was calculated with the mean SPAD reading for each plant based on the formula $(C - T)/C$ (Deol et al. 2001) where C is the SPAD measurement from the control and T is the SPAD measurement from infested plants.

GAS-EXCHANGE RESPONSES

A portable photosynthesis system (model LI-6400, LI-COR, Lincoln, Nebraska, USA) was used to measure all plants in the study. Methods closely followed those of Franzen et al. (2007), Gutsche et al. (2009), and Paudyal et al. (2019). Measures with the LI-COR 6400 were taken outside between 11:10 AM and 2:15 PM on a sunny d (d 15) with air temperatures of approximately 25 °C after plants were taken from the growth chamber and allowed to acclimate for approximately 1 h. Net photosynthetic rate (µmol CO_2 $m^{-2}s^{-1}$) and stomatal conductance (mol H_2O $m^{-2}s^{-1}$) were measured at 1,200 µmol photons $m^{-2}s^{-1}$ light intensity and a reference carbon dioxide of 400 ppm generated from a 12-g carbon dioxide cylinder connected to the meter.

DATA ANALYSES

All analyses were performed using SigmaPlot 11.0 (Systat Software, Erkrath, Germany). Response to light conditions and to the presence of aphids were examined by cultivar. Significance was when $\alpha = P < 0.05$. All response data first were checked for normality and then were compared using either ANOVA, followed by a Tukey test for normal data or Kruskal Wallis ANOVA to compare median values followed by a Tukey test when differences were detected for data that were not normally distributed. Whether ANOVA or Kruskal-Wallis ANOVA was performed, means ± 1 SE are presented in results.

Results

The light-emitting diode panel produced 2 primary emissions that were centered near 450 nm (blue) and 636 nm (red). Both emission peaks had similar widths, with full width at half maximum values of approximately 100 nm and 120 nm for the blue and red emissions, respectively (Fig. 1). Light intensity measures at plant height were 261.5 µmol (15 s average) with the quantum sensor and 27.1 lux (15 s average) with the photometric sensor for conventional lights, and 7,166 µmol (15 s average) with the quantum sensor and 172.65 lux (15 s average) with the photometric sensor for light-emitting diodes.

Sorghum cultivars grown under conventional light differed morphologically from those grown under light-emitting diodes both as controls and when exposed to aphid feeding (Figs. 2 & 3). Plants from all cultivars were tallest when grown under conventional light and were approximately twice as tall as the same plants grown under light-emitting diodes (Table 1). When exposed to aphid feeding

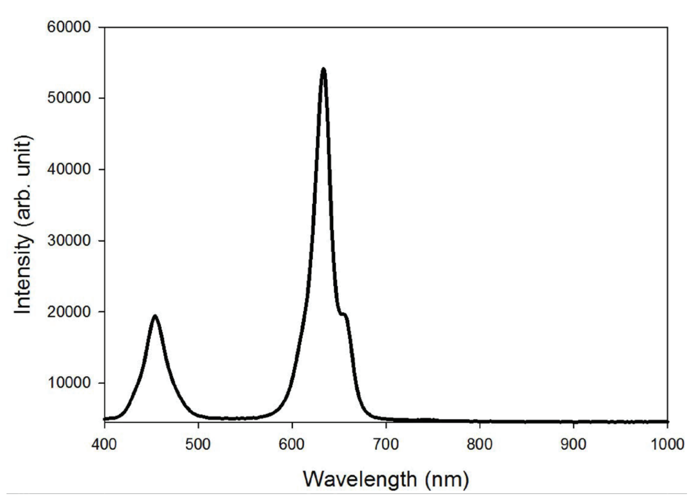

Fig. 1. Light emission spectrum of the 9 band 60-watt light-emitting diode grow panels over the visible spectrum and into the near infrared.

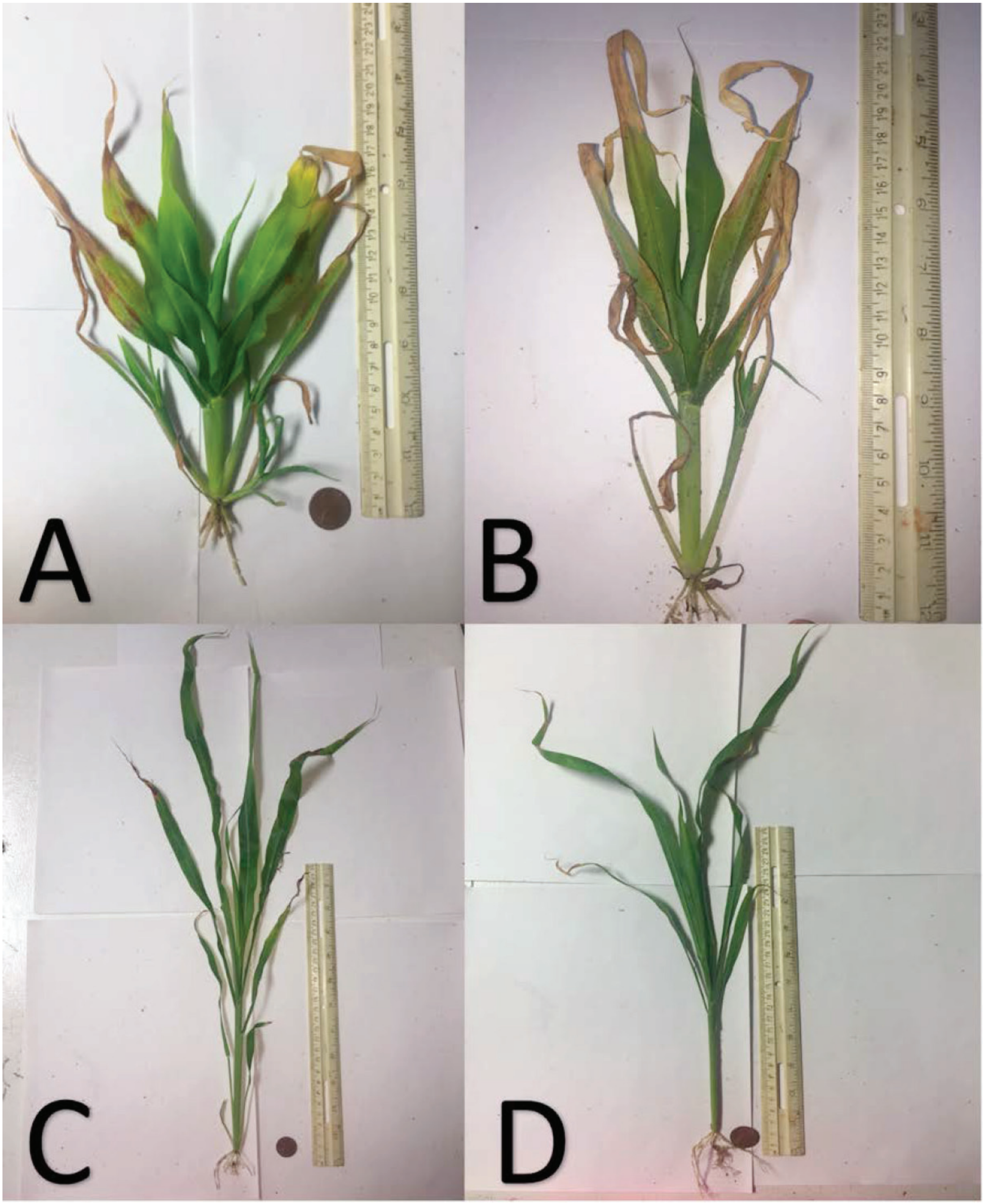

Fig. 2. Resistant sorghum variety TX-2783 across 4 treatments: (A) control under light-emitting diodes; (B) infested under light-emitting diodes; (C) control under conventional lights; (D) infested under conventional lights. Plants were infested with sugarcane aphids and assessed 15 d post infestation.

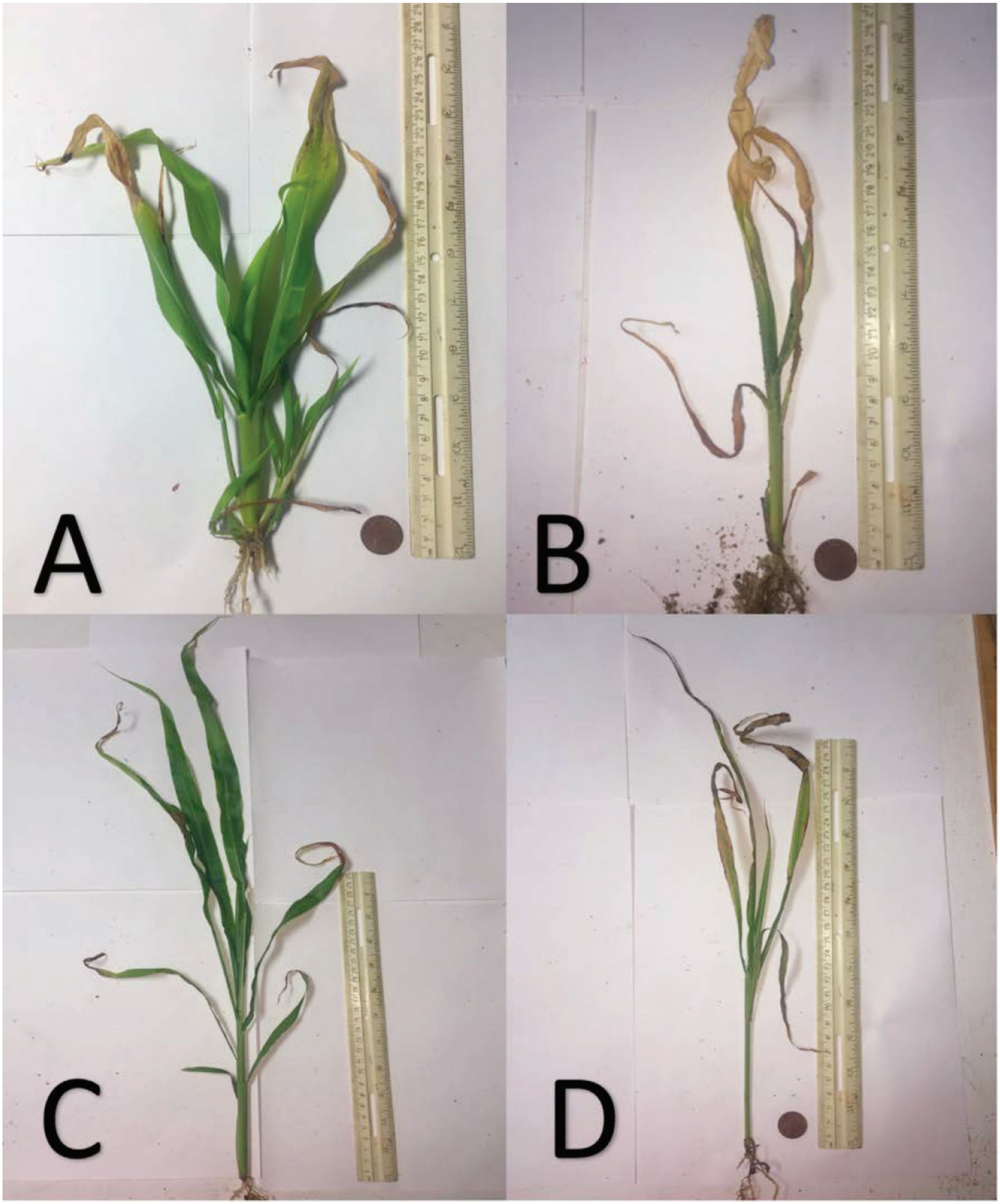

Fig. 3. Susceptible sorghum variety KS-585 across 4 treatments: (A) control under light-emitting diodes; (B) infested under light-emitting diodes; (C) control under conventional lights; (D) infested under conventional lights. Plants were infested with sugarcane aphids and assessed 15 d post infestation.

Table 1. Effect of light-emitting diodes and sugarcane aphid on plant response by 4 cultivars of *Sorghum bicolor* at 15 d after infestation. Numbers are mean ± SE.

		Plant height (cm)			
		TX-7000	KS-585	TX-2783	DKS-37-07
Conventional	Control	57.8 ± 0.64 a	55.8 ± 0.59 a	58.0 ± 1.2 a	56.5 ± 0.79 a
	Infested	40.9 ± 1.85 b	45.5 ± 0.75 b	53.6 ± 1.38 b	52.5 ± 0.74 b
Light-emitting diode	Control	29.5 ± 0.52 c	26.6 ± 0.61 c	23.9 ± 0.71 c	24.9 ± 0.8 c
	Infested	24.7 ± 1.16 d	27.6 ± 0.72 cd	26.3 ± 0.77 cd	33.6 ± 1.18 d
		df = 3; *H* = 39.046	df = 3; *F* = 450.19	df = 3; *H* = 38.844	df = 3; *F* = 279.76
		P < 0.0001	*P* < 0.001	*P* < 0.001	*P* < 0.001
		Leaf number			
Conventional	Control	8.0 ± 0.0 a	7.0 ± 0.0 a	8.0 ± 0.0 a	7.0 ± 0.0 a
	Infested	5.0 ± 0.0 a	5.0 ± 0.0 a	6.0 ± 0.0 a	6.2 ± 0.11 a
Light-emitting diode	Control	15.3 ± 0.8 b	13.6 ± 0.63 b	15.4 ± 0.50 b	14.0 ± 0.58 b
	Infested	10.8 ± 0.59 b	7.8 ± 0.22 b	12.3 ± 0.46 b	9.6 ± 0.62 b
		df = 3; *H* = 42.979	df = 3; *H* = 43.602	df = 3; *H* = 44.193	df = 3; *H* = 41.227
		P < 0.001	P < 0.001	P < 0.001	P < 0.001
		Leaf width (mm)			
Conventional	Control	2.1 ± 0.06 a	1.6 ± 0.04 a	1.9 ± 0.04 a	1.9 ± 0.04 a
	Infested	1.0 ± 0.03 b	1.3 ± 0.05 b	1.4 ± 0.03 b	1.5 ± 0.04 b
Light-emitting diode	Control	3.0 ± 0.08 c	3.1 ± 0.08 c	2.9 ± 0.03 c	2.9 ± 0.04 c
	Infested	2.3 ± 0.07 d	2.4 ± 0.03 d	2.4 ± 0.06 d	2.7 ± 0.07 d
		df = 3; *F* = 169.77	df = 3; *F* = 206.99	df = 3; *F* = 253.15	df = 3; *F* =180.905
		P < 0.001	P < 0.001	P < 0.001	P < 0.001
		Damage rating			
Conventional	Control	1.0 ± 0.0 a	1.0 ± 0.0 a	1.0 ± 0.0 a	1.0 ± 0.0 a
	Infested	6.2 ± 0.29 bc	6.67 ± 0.19 b	2.0 ± 0.0 bc	2.0 ± 0.12 a
Light-emitting diode	Control	3.3 ± 0.13 b	3.8 ± 0.41 a	3.3 ± 0.14 ab	2.6 ± 0.15 a
	Infested	7.9 ± 0.15 c	7.9 ± 0.15 c	6.5 ± 0.25 abc	5.7 ± 0.39 b
		df = 3; *H* = 44.17	df =3; *H* = 42.618	df =3; *H* = 44.941	df = 3; *H* = 42.517
		P < 0.001	P < 0.001	P < 0.001	P < 0.001

Response of each cultivar was checked for normality and then compared with either ANOVA (*F* value) or Kruskal Wallis ANOVA (*H* value) followed by a Tukey test when differences were detected. Columns with the same letters are not significantly different (*P* > 0.05).

under conventional lights, plant heights were reduced most for the susceptible cultivars TX-7000 and KS-585 (30% and 19%, respectively) compared to the plant heights of the resistant cultivars TX-2783 and DKS-37-07 (about 7% each). However, when plants were grown under light-emitting diodes and exposed to aphid feeding, plant heights were significantly increased for both resistant cultivars compared to the same cultivars grown under light-emitting diodes alone (Table 1). In contrast, the susceptible variety TX-7000 was shortest overall under light-emitting diodes with aphids, whereas DKS-37-07 heights were similar for plants under light-emitting diodes alone and when exposed to aphids under light-emitting diodes.

Populations of the sugarcane aphid differed significantly by light type for 3 of the 4 tested cultivars (Fig. 4). Surprisingly, aphid numbers were lower on known susceptible cultivars (TX-7000 and KS-585) compared to populations on the known resistant cultivars (TX-2783 and DKS-37-07). Susceptible plant health declined over the 15-d trial and aphid survival diminished. Susceptible plants grown under light-emitting diodes had the least aphids because plants could not maintain the aphids. For both resistant cultivars, the numbers of sugarcane aphids were significantly higher under light-emitting diodes (Fig. 3), reaching more than 300 per seedling for DKS-37-07.

All 4 sorghum entries, produced twice as many true leaves when grown under light-emitting diodes than for the same entries grown under conventional lights (Table 1). Aphid feeding reduced the num-

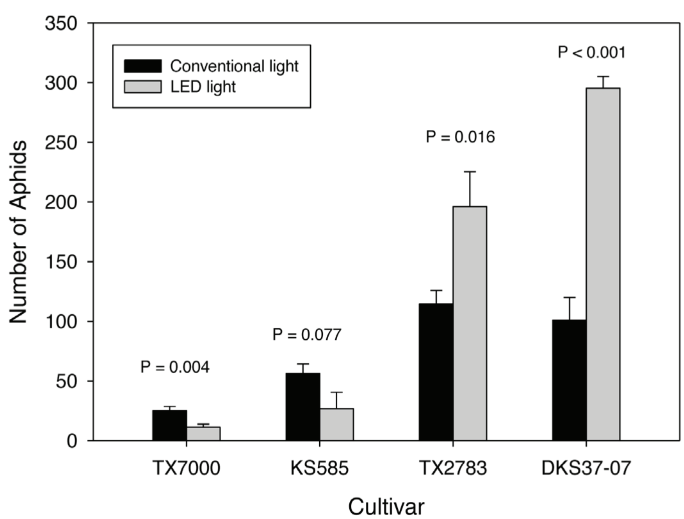

Fig. 4. Mean ± SE number of sugarcane aphids per plant 15 d after infestation when grown for resistant (TX-2783 and DKS-37-07) and susceptible (TX-7000 and KS-585) sorghum cultivars grown under either conventional or light-emitting diodes. *P*-values represent results of a Student's *t*-test (df = 22) for each variety.

ber of leaves by an average of 1 to 3 under conventional lights and by 3 to 5 under light-emitting diodes; however, the change in leaf numbers was not significant. Under light-emitting diodes, all sorghum cultivars produced wider leaves suggesting a plant response to absorb more light (Table 1). Infestation with aphids significantly reduced leaf width under both conventional light and light-emitting diodes although the leaf width of DKS-37-07, a resistant cultivar changed the least (Table 1).

When sorghum plants were rated for damage, all cultivars were healthy when grown under conventional lights in the absence of aphids (Table 1). Aphid feeding significantly increased damage ratings for all cultivars except DKS-37-07, a known resistant variety. Plants grown under light-emitting diodes had significantly higher damage ratings and the damage ratings increased significantly when exposed to aphids under light-emitting diodes for all cultivars, including DKS-37-07 (Table 1).

Damage rating scores for control plants in the conventional lighting were lower than damage ratings for both the susceptible and resistant entries grown under light-emitting diodes (Table 1), and the same pattern was observed for the infested plants. Damage ratings were from 1.5 to 4.5 lower for infested plants under conventional lighting as compared to the infested damage ratings for plants under light-emitting diodes.

Light-emitting diodes reduced the photosynthetic rates of KS-585 (a susceptible variety) and TX-2783 (a resistant variety) but was similar for the other cultivars tested (Fig. 4). As anticipated, infestation with sugarcane aphid significantly reduced photosynthetic rates for the susceptible cultivars but not for the resistant cultivars. For all cultivars tested, including resistant cultivars, infestation with aphids under light-emitting diodes significantly reduced photosynthetic rates (Fig. 5).

Similar to observations of photosynthetic response to light type, stomatal conductance was unaffected under light-emitting diodes for TX-7000 but was significantly reduced for the other cultivars (Fig. 6). Aphid feeding reduced stomatal conductance for all cultivars except TX-2783 under conventional light.

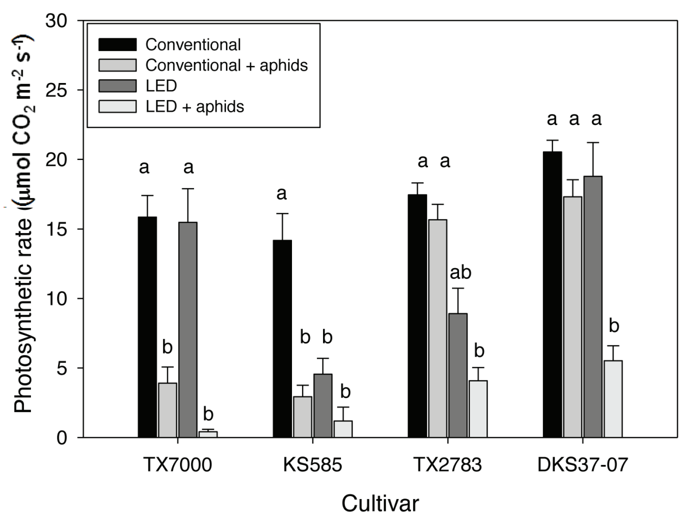

Fig. 5. Mean ± SE photosynthetic rates (µmol CO2 m^{-2} s^{-1}) of resistant (TX-7000 and KS-585) and susceptible (TX-2783 and DKS-37-07) sorghum cultivars grown under either conventional or light-emitting diodes. All plants were measured at 15 d after infestation with sugarcane aphids. Bars with different letters are significantly different (Kruskal-Wallis ANOVA, df = 3; $H > 27.14$; $P < 0.01$).

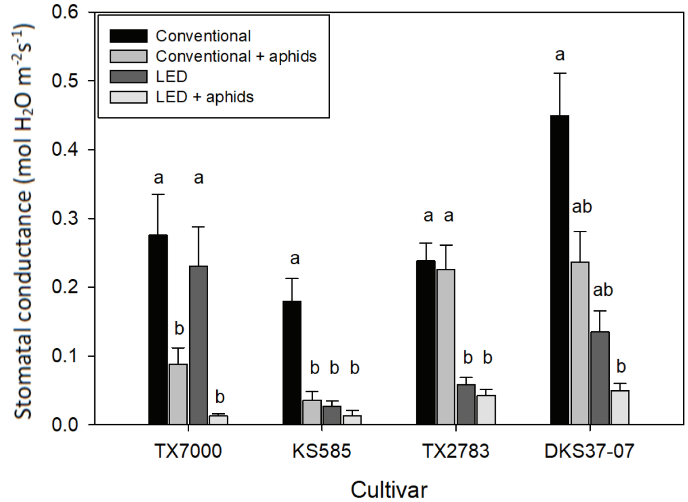

Fig. 6. Mean ± SE stomatal conductance (mol H2O m^{-2} s^{-1}) at 15 d after infestation under light-emitting diode and conventional lights. Bars with different letters are significantly different (Kruskal-Wallis ANOVA, df = 3; $H > 24.13$; $P < 0.01$).

When the amount of chlorophyll was measured in control plants compared to those exposed to aphid feeding, the resistant cultivars lost about half as much chlorophyll as the susceptible cultivars under conventional lights. All cultivars except KS-585 lost significantly more chlorophyll under light-emitting diodes (Fig. 7). For KS-585, a similar amount of chlorosis was observed for both types of lights whereas TX-2783 plants grown under light-emitting diodes lost 3 times more chlorophyll and nearly as much as the susceptible TX-7000 did under conventional lighting.

Discussion

In this study, 4 identical growth chambers were available only for a period allowing a single trial. Following the methods of Limaje et al. (2019), we used 2 chambers with conventional lights and 2 with light-

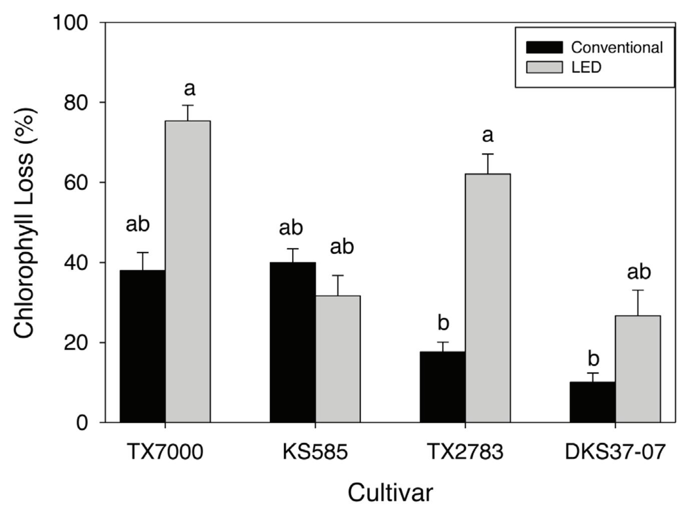

Fig. 7. Mean ± SE chlorophyll loss at 15 d after infestation under light-emitting diode and conventional lights (control-infested)/control. Different letters represent significant differences ($P < 0.001$) with a Kruskal-Wallis ANOVA followed by Dunn's multiple comparison test ($H = 62.629$; df = 7).

emitting diodes, with 1 chamber each receiving plants infested with aphids and the other serving as a control. Within each chamber we tested 12 plants from each of 4 varieties using a randomized complete block design for placement. All plants were placed on the same growth chamber shelf. This design constraint leads to the possibility of uncontrolled differences among chambers and pseudo-replication because the trial was conducted once. However, growth chamber conditions were monitored daily and the chamber receiving each light treatment was randomly assigned initially. Light measures within chambers were very similar, supporting the conclusion that our results relate to lighting condition and the presence of aphids rather than uncontrolled differences among chambers.

The light-emitting diodes used in these experiments affected the plant height, number of true leaves, leaf widths, and plant physiology of 4 varieties of sorghum (Figs. 2 & 3; Table 1) compared to plants grown under conventional lighting. Although different brands of light-emitting diodes were used between the Limaje et al. (2019) study and this one, the light spectra were similar (Fig. 1). Limaje et al. (2019) previously documented unusual sorghum growth and differential response to herbivory by the sugarcane aphid under light-emitting diodes. However, the physiological mechanism for plant differences and determination of consistency of results across cultivars was not elucidated. The light spectra used by Limaje et al. (2019) were different than that used in the current study, and although results for growth form were similar, sorghum grown under light-emitting diodes by Limaje et al. (2019) had unusual colors including purple and pink that were not observed in this study. Park (2018) reported unusual colors in some tested plants associated with higher intensities of light-emitting diode red-blue wavelengths. In the current study, the absence of different sorghum leaf colors between light-emitting diodes and conventional light trials suggests that the amount of photosynthetically active radiation was more similar.

In the Limaje et al. (2019) study, similar numbers of sugarcane aphids were observed on sorghum grown under conventional light compared to sorghum grown under light-emitting diodes. In contrast in this study, the light type and sorghum cultivar influenced aphid numbers, reducing aphids on susceptible cultivars under conventional lighting but increasing aphid numbers on resistant varieties under light-emitting diodes(Fig. 4). Low aphid numbers on the susceptible sorghum likely are explained by plant condition. Susceptible varieties had damage ratings of 6 to 8 under conventional and light-emitting diodes, respectively (Table 1), and likely could not support sugarcane aphid growth and reproduction. In contrast, resistant varieties supported larger numbers of aphids (about 100 per plant under conventional lighting). Aphid numbers significantly increased on resistant varieties under light-emitting diodes, suggesting that the plants' resistance mechanisms were compromised under the light-emitting diodes conditions (Fig. 4). Despite higher numbers of aphids, the resistant sorghum damage ratings were still lower than those of the susceptible varieties even under light-emitting diodes.

Plants grown under light-emitting diode grew 2 to 3 times more true leaves, regardless of being infested or not infested with sugarcane aphid when compared to plants under conventional lights. Damage ratings were increased by 21 and 16%, respectively, when the 2 susceptible sorghums (TX-7000 and KS-585) were grown under light-emitting diodes, infested, and compared to plants grown under conventional lights and infested. Damage ratings for resistant sorghums were 69 and 65% greater for infested and resistant sorghums TX-2783 and DKS-37-07, respectively. Therefore, both the light source (light-emitting diode versus conventional) and the known resistant or susceptible sorghum used in the study influenced damage ratings but to a lesser extent for resistant types of sorghum.

When sugarcane aphids were present, both leaf width and number of true leaves were reduced as has been observed for many studies where sugarcane aphid damage was assessed in the effort to find host plant resistance (Armstrong et al. 2015; Paudyal et al. 2019, 2020) (Table 1). This is an important outcome of both Limaje et al. (2019) and the present experiments because plants often are screened for potential resistance in greenhouse or growth chamber studies, and depending on light conditions, potentially susceptible or resistant genotypes could be misinterpreted.

The effects of lighting on sorghum physiology were not consistent across cultivars that were either resistant or susceptible. The susceptible KS-585 and the resistant TX-2783 had significantly lowered photosynthetic rates when grown under light-emitting diodes without the presence of aphids (Fig. 3). Stomatal conductance rates also were differed by cultivar and lighting condition, being highest for DKS-37-07 and similar for the other cultivars under conventional light (Fig. 4). Light-emitting diodes reduced the stomatal conductance rates for all cultivars except TX-7000. With infestation of aphids, the resistant cultivars under light-emitting diodes had significantly reduced photosynthetic rates, whereas both resistant cultivars maintained similar rates under conventional lighting (Fig. 3). Resistant cultivars also maintained greater stomatal conductance rates under conventional lighting in the presence of aphids. With light-emitting diodes and aphids, all tested cultivars had significantly lower stomatal conductance. The observed differences in photosynthetic rates and stomatal conductance with aphid infestations are not explained directly by loss of chlorophyll from aphid feeding, although chlorophyll losses were higher under light-emitting diodes for all cultivars except for the resistant KS-585.

Light-emitting diodes has been shown to benefit a number of plant species, including Solanaceae (Brown et al. 1995), spinach (*Spinacia oleracea* L. [Amaranthaceae]), radish (*Raphanus raphanistrum* L. [Brassicaceae]), lettuce (*Lactuca sativa* L. [Asteraceae]) (Yorio et al. 2001), and strawberry (*Fragaria* L. [Rosaceae]) (Nhut et al. 2003). In addition to promoting growth and yield, when lettuce seedlings were grown under blue light-emitting diodes, antioxidant activity was promoted which increased the overall growth of the seedlings (Johkan et al. 2010).

Less research has been conducted on plants with C4 photosynthetic pathways grown under light-emitting diodes, although to date, only sorghum has been documented to have negative responses. In C4 photosynthesis, there are 3 subtypes of decarboxylation. NADP-ME (NADP-dependent malic enzyme), NAD-ME (NAD-dependent malic enzyme) and PEPCK (phosphoenolpyruvate carboxykinase) as described by Hatch (1987). Wheat, *Triticum aestivum* L. (Poaceae), which is a C4 plant (Casati et al. 1997), had increased photosynthetic activity, number of tillers, biomass, and overall yield when grown under light-emitting diodes (Monostori et al. 2018). Although sorghum also displayed increased growth in leaf number and leaf width (Table 1), which could be argued to be favorable, decreased photosynthetic rates (Fig. 5), and reduced stomatal conductance (Fig. 6) also occurred when grown under light-emitting diodes even in the absence of aphids. It is important to note that there are different subtypes of the C4 photosynthesis cycle. Sorghum has the NAD-ME C4 pathway (Rao & Dixon 2016), whereas wheat has the C4 subtype of NADP (Casati et al. 1997). Thus, the specific differences in decarboxylation may be the key to affecting the growth of sorghum under light-emitting diodes.

Tobacco, *Nicotiana tabacum* L. (Solanaceae), a C3 plant, shows C4 photosynthesis pathways in the vascular bundles of the stem and petioles (Hibberd & Quick 2002). Both sorghum and tobacco use the same NAD-ME C4 pathway (Rao & Dixon 2016). Light-emitting diodes promote growth of tobacco plants and reduces the membrane lipid peroxidation damage of the plant (Jun et al. 2014). Perhaps unlike sorghum, tobacco experiences positive growth effects from being grown under light-emitting diodes because it does not completely rely on the NAD-ME C4 pathway as does sorghum. More work should be done with sorghum and the NAD-ME pathway to determine if the observed negative effects are based on the inability of NAD-ME to compensate efficiently when grown under light-emitting diodes.

A key outcome of this study is the effects that light-emitting diodes had on resistant and susceptible sorghum when aphids were present. Overall, as anticipated when aphids were on the plant, the plant displayed reduced measurements across evaluated characteristics (Table 1). However, plant height was significantly greater for DKS-37-07 when infested with aphids and grown under light-emitting diodes compared to the un-infested plants (Table 1). It is possible that early infestation of aphids promoted plant response leading to taller plants, and then damage increased until physiological measures were taken at d 15. Thus, the interaction between aphid feeding and plant growth under light-emitting diodes should be investigated further, especially because these plants had more chlorosis (Fig. 5) and lower photosynthetic rates (Fig. 3). At a minimum, in future trials aimed at identifying plant resistance to herbivores, the effects of experimental lighting should be considered.

The effects of light-emitting diodes on herbivores also requires more research. Aphids are small and soft-bodied, and altered light wavelengths may impact their behavior or physiology. Previously, Limaje et al. (2019) noted differences in behavior of aphids in light-emitting diode experiments compared to those in conventional light treatments. The cabbage aphid, *B. brassicae*, and green peach aphid, *M. persicae*, also have been documented to be affected by light-emitting diodes (Rechner et al. 2016). When grown on broccoli (*Brassica oleracea* var. *italica* L.; Brassicaceae), the cabbage aphid decreased growth and reproduction, while the green peach aphid increased reproduction and population growth (Rechner et al. 2016).

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