Oecologia (2020) 193:503–510
https://doi.org/10.1007/s00442-020-04679-9

GLOBAL CHANGE ECOLOGY – ORIGINAL RESEARCH

Interactions between artificial light at night, soil moisture, and plant density affect the growth of a perennial wildflower

Melissa H. Hey[1] · **Elizabeth DiBiase**[2] · **Deborah A. Roach**[3] · **David E. Carr**[1,4] · **Kyle J. Haynes**[1,4]

Received: 6 September 2019 / Accepted: 3 June 2020 / Published online: 12 June 2020

Abstract

Artificial light at night (ALAN) has been shown to alter aspects of plant growth, but we are not aware of any studies that have examined whether the effects of ALAN on plants depend upon the backdrop of variation in other abiotic factors that plants encounter in field populations. We conducted a field experiment to investigate whether ALAN affects the growth and anti-herbivore defenses of common milkweed, *Asclepias syriaca*, and whether the effects of ALAN are influenced by plant density or soil moisture content. Artificial light at night, soil moisture, and plant density were manipulated according to a split-plot factorial design. Although increasing soil moisture by watering had no significant effects on latex exudation, attributes of plant growth generally responded positively to watering. The basal stem diameter (BSD) and height of plants were affected by ALAN × soil moisture interactions. For both of these variables, the positive effects of ALAN were greater for plants that were not watered than for plants that were. Basal stem diameter was also affected by an ALAN × plant density interaction, and the positive effect of ALAN on BSD was greater in the low-density treatment than in the high-density treatment. Our results demonstrate that the effects of ALAN on plant growth can be altered by soil moisture and plant density. Consequently, the effects of ALAN on plants in nature may not be consistent with existing frameworks that do not account for critical abiotic variables such as water availability or biotic interactions between plants such as competition.

Keywords Milkweed · Sensory pollution · Light pollution · Precipitation · Community ecology

Introduction

Artificial light at night (hereafter ALAN) currently affects nearly a quarter of Earth's terrestrial surface (Longcore and Rich 2004; Falchi et al. 2016). Over the past decade, there has been growing interest in understanding the biological and ecological effects of this pervasive sensory pollutant (Gaston et al. 2013; Falchi et al. 2016). It has adverse effects on animal behavior, for instance redirecting sea turtle hatchlings towards build structures rather than the ocean (Witherington and Martin 2000) and reducing foraging behavior in New Zealand weta (Farnworth et al. 2018). ALAN also changes local abundances of terrestrial invertebrates (Davies et al. 2012, 2017). Effects of ALAN on demographic processes in animal populations have also been found (Firebaugh and Haynes 2019). Much less is known about the effects of ALAN on wild plants (Gaston et al. 2013; Bennie et al. 2016) despite the fact that as photomorphogenic organisms, ALAN is likely to exert wide-ranging effects on plant growth, physiology, and phenology (Briggs 2006; Gaston et al. 2013; Bennie et al. 2015, 2016).

For plants, many of the ecological consequences of ALAN that have been found involve the alteration of biotic interactions. In contrast, little is known about whether the effects of ALAN depend upon variation in other abiotic factors that are critical to the performance of plants in

---

Communicated by Casey P. terHorst.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00442-020-04679-9) contains supplementary material, which is available to authorized users.

✉ Melissa H. Hey
mh5rd@virginia.edu

[1] Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22904, USA

[2] Pennsylvania Department of Agriculture, Harrisburg, PA 17110, USA

[3] Department of Biology, University of Virginia, Charlottesville, VA 22904, USA

[4] Blandy Experimental Farm, University of Virginia, 400 Blandy Farm Lane, Boyce, VA 22620, USA

nature, such as temperature or soil moisture. Some previous research suggests that interactive effects between ALAN and moisture availability should be explored. For example, plants exposed to continuous light exhibit loss of proper stomatal functioning (Kwak et al. 2017, 2018). Improper stomatal functioning can decrease plant water use efficiency, making plants more susceptible to drought-related stress (Lawson and Blatt 2014). Moreover, the effects of continuous light on plant stomata may be particularly strong in the presence of broad-spectrum LED lights, because plant photoreceptors triggered by blue light are associated with stomatal movements (Kami et al. 2010; Hart 1988; Briggs 2006). Such an effect of ALAN on plant stomata might adversely impact plant growth or survival.

ALAN has been shown to affect a number of biotic interactions. These include plant–herbivore interactions (Bennie et al. 2015, 2018; Grenis and Murphy 2019), plant–pollinator interactions (Knop et al. 2017; Macgregor et al. 2017), and tri-trophic interactions between plants, their herbivores, and parasitoids (Sanders et al. 2015). In a multi-year field experiment, Bennie et al. (2017) found that ALAN altered plant species composition in a semi-natural grassland. While they emphasized that the shifts in species composition could be explained by direct effects of ALAN on plant physiology that influence growth form, resource allocation, and phenology, they did not rule out indirect effects mediated by biotic interactions. Furthermore, Bennie et al. (2016) argued that there is a need for more study on whether ALAN can affect plant communities through alteration of competition and other biotic interactions. Given that ALAN can directly induce plants to increase aboveground vegetative growth (Cathey and Campbell 1976), it is plausible that ALAN could intensify competition among neighboring plants for access to sunlight. Direct effects of ALAN on vegetative growth could, in turn, also increase plant demands for water and other soil nutrients, which could further increase competition among neighboring plants. Studying the vegetative growth of plants grown under ALAN at different densities and resource availabilities would be an important first step in understanding the potential effects of ALAN on competition in plants.

Our objective was to test for potential interactive effects of ALAN with soil moisture and plant density on plant growth and defense. We selected common milkweed, *Asclepia syriaca*, as our model organism because it is an herbaceous perennial with a range that overlaps many of the areas in the contiguous United States with the highest intensities of ALAN. As it often occupies recently disturbed habitats, *A. syriaca* is common along transportation networks (Nichter and Gregory 2018) and, therefore, is exposed to ALAN from roadway lighting and automobile headlights.

Our objective was achieved using a manipulative field experiment. We manipulated ALAN (present or absent), plant density (one or three plants per pot), and soil moisture (plants provided supplemental water or received only ambient precipitation) and then monitored several attributes of plant growth over four weeks. We also measured exudation of latex, an anti-herbivore defense, during the third week of exposure to the treatments and biomass per plant at the conclusion of the experiment. We predicted that ALAN would have a positive effect on plant growth but a negative effect on plant defenses. Specifically, we expected that ALAN would stimulate plants to grow taller than their unlit counterparts, due to the stem-elongation response of some plants to continuous light (Cathey and Campbell 1975). We expected that ALAN-induced increases in growth would be weaker in plants grown at the higher density because competition for limiting resources would constrain growth. We also predicted that providing supplemental water would increase plant size, but that the effects would be smaller under ALAN because we expected ALAN-induced changes in stomatal functioning (Kwak et al. 2017, 2018) to increase water stress (Greenham and McClung 2015; Robertson et al. 2009). Based upon growth-defense tradeoff theory (Lind et al. 2013; Huot et al. 2014; Züst and Agrawal 2017), we anticipated that increased aboveground plant growth due to ALAN would lead to a weakening of plant defenses. Finally, because latex production in common milkweed is known to increase with soil moisture availability (Couture et al. 2015), we anticipated that increased water loss due to ALAN would counteract positive effects of watering on latex production.

Methods

Study system

Common milkweed, *Asclepias syriaca*, is defended from herbivore attack by both physical and chemical defensive mechanisms and is, therefore, typically attacked only by a small group of specialist insect herbivores. Its physical defenses consist of non-glandular leaf trichomes and latex, a sticky substance exuded when aboveground tissues are damaged. The species' secondary metabolites (cardenolides) serve as a chemical defense as they are highly toxic cardiac glycosides capable of triggering cardiac arrest (Agrawal and Malcolm 2002; Agrawal and Konno 2009).

Experimental design

The field experiment was carried out in 2017 at University of Virginia's Blandy Experimental Farm (Boyce, VA) in 10 1-m-diameter plots that were created in 2016. We manipulated ALAN, soil moisture, and plant density according to a split-plot factorial design, with ALAN manipulated at the level of the plots, and plant density and soil moisture manipulated at the level of pots within the plots. Artificial light at night (from dusk to dawn) was added to half of the 10 field plots (chosen at random). In plots assigned to receive ALAN (hereafter ALAN plots), the light was emitted by a single broad-spectrum (4922 K) 12 W LED (Bullet®, RAB Lighting Inc., Northvale, New Jersey, USA) suspended 3 m above the ground on a light post (Online Resource Figs. 1, 2). Dummy light posts with no LED were installed over the plots receiving only ambient light. Based on light-meter (Extech LT300, FLIR® Systems, Inc., Wilsonville, Oregon, USA) measurements taken between civil twilight and dawn at a height of 1 m above the ground (roughly 60–80 cm above the plant canopy), illumination was 52.75 ± 4.41 (mean ± SD) lux in the ALAN plots, which approximates light intensities experienced under streetlights (Bennie et al. 2016; Jin et al. 2017). Because light intensity was measured above the plant canopy, we can assume illumination of the experimental plants by the LEDs was somewhat lower than the recorded measurements. Illuminance in the ambient-lit plots was 1.2 ± 0.14 lx.

To examine whether intraspecific competition among plants alters the effects of ALAN, seedlings were grown in pots (11.3 L) at two different densities, one (low-density treatment) or three plants (high-density treatment) per pot, with plants randomly assigned to each density treatment. The plants used in the experiment were grown from seeds collected at Blandy Experimental Farm in fall 2016, cold stratified during the winter, and germinated in May 2017. After growing in a greenhouse for 7 weeks, the plants were transplanted to the pots, which were filled with moistened soil (Sungrow Horticulture Professional Growing Mix, Sungrow Horticulture, Sun Gro®, Agawam, Massachussetts, USA). Four pots, two from each of the two plant density treatments, were randomly assigned to each of the ten field plots. The pots were sunk into pre-drilled holes, so that the soil surface within each pot was flushed with the surrounding soil surface.

Soil moisture was manipulated with weekly additions of approximately 3.8 L of water to one of the two pots per density treatment in each plot. The other pots received no supplemental water.

Data collection

We assessed the effects of ALAN, plant density, and soil moisture on plant growth based on measures of plant height, basal stem diameter, and area of the newest fully extended leaf taken for every experimental plant once per week over 4 weeks. Because the leaves are roughly triangular in shape, leaf area was estimated as $½ \times l \times w$, where l was the length of a leaf w was its maximum width.

We also evaluated the effects of the experimental factors on total (aboveground + belowground) biomass per plant. This was measured via destructive harvesting at the conclusion of the experiment, after 4 weeks of exposure to the experimental manipulations. For each individual, we cut the stem at the soil level and then cleared the soil from roots first by gentle brushing with a paintbrush, followed by rinsing with water. The roots and shoots were dried at 40 °C for 66 h and then weighed to determine the total biomass of each individual.

To examine effects of the experimental factors on plant defenses, we measured the amount of latex exuded (grams, dry weight) by one leaf on each plant during the third week of the experiment. The amount of latex present in milkweed leaves has previously been linked to plant water status (Agrawal et al. 2014). The experiment was carried out during a particularly wet season at BEF, July rainfall was approximately 19.05 cm, 7.62 cm higher than the average recorded over the previous ten years at the site. Latex was collected only once from each plant to limit damage to the plants. Latex was collected from each plant's youngest fully extended leaf following methods outlined in Agrawal et al. (2014). The leaf was cut 5 mm from the tip with scissors and latex was allowed to flow onto pre-weighed filter paper (1 cm^2) until flow stopped, about ten seconds. After air drying the filter papers at room temperature for 2 days, they were weighed a second time to determine latex dry weights.

During week 2 of the experiment, we noticed foliar damage on some of the experimental plants. Beginning that week, we assigned each plant a damage score every week for the remainder of the experiment. The damage score ranged from 0 to 100% in increments of 20%; 0% damage was recorded when there was no visible damage to any foliar tissue and 100% damage was recorded when nearly all leaves were severely damaged or removed.

Statistical analyses

To avoid pseudoreplication due to the non-independence of the multiple plants growing within the same pot in the high-density treatment (three plants per pot vs. one plant per pot in the low-density treatment), all statistical analyses used only the mean value of a response variable within each high-density pot (e.g., mean height of the three plants). For attributes of plant growth or defense that could be sampled non-destructively, we used a repeated-measures statistical design because it provides greater statistical power for a given number of study subjects than does a design in which each subject is only sampled once, such as at the conclusion of the experiment Guo et al. (2013).

Repeated-measures analyses using linear mixed-effects (LME) models were used to test the interactive effects of ALAN with soil moisture and plant density on plant height, BSD, and leaf area. The fixed effects in the models included ALAN, soil moisture, plant density, ALAN × soil moisture, ALAN × plant density, and week. We also included herbivore damage score (average score in each pot) as a covariate in our models. We modeled the random effect of plot across time (the interaction between plot and week) using uncorrelated random intercepts and slopes. Models with more complex random effects structures (e.g., correlated intercepts and slopes) failed to converge. To normalize the LME model residuals and to reduce heterogeneity of variance, basal stem diameter and leaf area were $\log(x + 1)$ transformed. Plant height was Box-Cox transformed, using an exponent (λ) of 0.88.

The effects of ALAN, soil moisture, plant density, and ALAN × soil moisture, ALAN × plant density interactions on latex exudation and total biomass per plant were also assessed using LME models. Herbivore damage score was included as a covariate. We modeled the random effect of plot as random intercepts. Prior to the analyses, latex dry mass and total biomass were $\log(x + 1)$ transformed to improve normality of the model residuals.

Given that we observed herbivore damage starting in the second week of the experiment, we also examined whether the presence/absence of herbivory was affected by the experimental factors (ALAN, soil moisture, and plant density) and their two-way interactions (ALAN × Soil Moisture, ALAN × Plant Density) in a repeated measures analysis using data from weeks 2 to 4. The analysis was conducted using a generalized linear mixed-effects model using a binomial distribution for the response variable and the logit link function. Week was included as a fixed effect. We modeled the random effect of plot across time using uncorrelated random intercepts and slopes.

All statistical analyses were carried out using R (R Core team 2019). The LME model fitting was carried out using the package 'lme4' (Bates et al. 2014). To test the statistical significance of the fixed effects, degrees of freedom were estimated using via Satterthwaite's method using the package 'lmerTest' (Kuznetsova et al. 2017).

Results

Table 1 Results of linear mixed-effects model on the effects of artificial light at night (ALAN), soil moisture, plant density, week (time since planting), herbivore damage, and some two-way interactions on the basal stem diameter (mm) of common milkweed

Source of variation	Estimate	S.E	*df*	*t*	*p*
ALAN (*A*)	0.049	0.032	70.62	1.523	0.132
Soil moisture (S)	0.141	0.021	135.16	6.716	< 0.001***
Density (*D*)	-0.017	0.021	132.54	-0.792	0.430
Week	0.128	0.013	90.48	9.851	< 0.001***
Damage	0.010	0.011	136.04	0.899	0.370
A × *S*	-0.081	0.030	134.68	− 2.720	0.007**
A × *D*	0.075	0.029	132.72	2.557	0.012*

*Significant at the $a = 0.05$ confidence level

**Significant at the $a = 0.01$ confidence level

***Significant at the $a = 0.001$ confidence level

Table 2 Results of linear mixed-effects model on the effects of artificial light at night (ALAN), soil moisture, plant density, week (time since planting), herbivore damage, and some two-way interactions on plant height (cm)

Source of variation	Estimate	SE	*df*	*t*	*p*
ALAN (*A*)	1.068	0.419	25.460	2.552	0.017*
Soil moisture (S)	1.286	0.285	136.390	4.507	< 0.001***
Density (*D*)	− 0.311	0.286	134.680	− 1.088	0.279
Week	0.399	0.159	136.810	2.514	0.013*
Damage	− 0.161	0.145	137.340	− 1.112	0.268
A × *S*	− 1.036	0.400	135.900	− 2.589	0.011*
A × *D*	0.685	0.399	134.620	1.719	0.088

*Significant at the $a = 0.05$ confidence level

**Significant at the $a = 0.01$ confidence level

***Significant at the $a = 0.001$ confidence level

Our repeated-measures analyses of effects of ALAN, watering, plant density, and their interactions revealed a variety of effects on different attributes of plant growth. Both plant height and BSD were affected by the ALAN × watering interaction (Tables 1, 2). Plant height was 14% higher, on average, under ALAN than under ambient light and 12% higher, on average, in pots that were watered than in pots that were not watered (receiving only ambient precipitation; Fig. 1, Table 2). The mean effect of watering on plant height was greater for plants under ambient light (20% increase) than those under ALAN (4% increase). Under ambient light, watering increased BSD by 13%; whereas, watering only increased BSD by 5% under ALAN. Basal stem diameter was also affected by a significant ALAN × plant density interaction. The mean effect of ALAN on BSD was greater in the low-density treatment (8%) than in the high-density treatment (2%). Leaf area was significantly increased by watering (Table 3, Fig. 1, Online Resource Fig. 3) and was the only growth variable where we found a significant negative relationship with herbivore damage.

Total (aboveground + belowground) biomass per plant at the conclusion of the experiment was increased by watering by an average of 25% ($t_{21.1} = 2.291$, $P = 0.032$; Fig. 2a, Table 4). However, plant biomass was not significantly affected by the other experimental factors or herbivore damage (Table 4).

Despite the fact that the dry mass of latex exuded was 40% higher on average from plants exposed to ALAN than from plants exposed to ambient light, latex exudation was

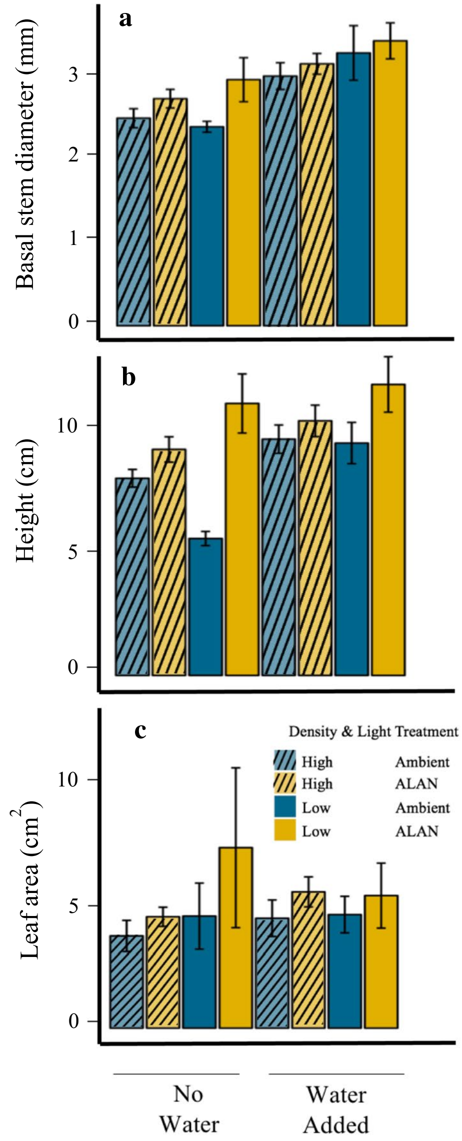

Fig. 1 Effects of artificial light at night (ALAN), plant density, and soil moisture on **a** basal stem diameter, **b** height, and **c** leaf area in the final week of data collection. Bars are means ± 1 SE

not significantly affected by ALAN (Table S1), likely due to high variability in this measure (Fig. 2b). Furthermore, we found no significant effects of any experimental factor or herbivore damage on latex exudation (Online Resource Table S1).

Table 3 Results of linear mixed-effects model on the effects of artificial light at night (ALAN), soil moisture, plant density, week (time since planting), herbivore damage, and some two-way interactions on leaf area (cm^2)

Source of variation	Estimate	SE	*df*	*t*	*p*
ALAN (*A*)	0.011	0.147	18.03	0.071	0.944
Soil moisture (S)	0.239	0.098	131.33	2.442	0.016*
Density (*D*)	−0.121	0.097	130.01	−1.247	0.215
Week	0.193	0.059	54.73	3.275	0.002**
Damage	−0.173	0.051	132.07	−3.371	0.001***
$A \times S$	−0.083	0.137	131.41	−0.603	0.548
$A \times D$	0.142	0.136	130.36	1.043	0.299

*Significant at the $a = 0.05$ confidence level

**Significant at the $a = 0.01$ confidence level

***Significant at the $a = 0.001$ confidence level

Discussion

This study revealed that ALAN can interact with soil moisture and plant density to affect aboveground plant growth. Consistent with our prediction, based on studies showing that ALAN can adversely affect stomatal functioning (Kwak et al. 2017, 2018), we found that positive effects of increasing soil moisture on plant growth (specifically basal stem diameter and plant height) were weaker under ALAN than under ambient light (Fig. 1a, b). Improper stomatal functioning can decrease plant water use efficiency (Lawson and Blatt 2014), the ratio of net carbon assimilation to transpiration. If ALAN inhibited proper stomatal functioning in our experiment, decreased efficiency in carbon assimilation could potentially explain why increasing soil moisture had a weaker positive effect on plant growth in plants under ALAN than ambient light. One caveat to this argument is that we did not observe the same interactive effects on total (aboveground + belowground) plant biomass. Nonetheless, these findings suggest there is a need to study the effects of ALAN on the water use efficiency of plants given the inextricable link between water use efficiency and primary productivity.

Latex exudation is associated with anti-herbivore defensive ability in common milkweed (Agrawal and Fishbein 2006; Van Zandt and Agrawal 2004). In our study, the mean dry weight of latex exuded from plants exposed to ALAN was 40% higher than from plants exposed to ambient light, but latex exudation was highly variable (Fig. 2b) and not significantly affected by ALAN or any other experimental factor. Herbivory might help to explain the high variability in latex exudation. Van Zandt and Agrawal (2004) demonstrated not only that latex production by common milkweed increases following herbivory, but also that the strength of the induced response in latex production differs between different specialist herbivores. It is possible that the variability in latex exudation that we observed was due to differences among the experimental plants in the intensity of herbivory or differences in the composition of attacking herbivore species. Given that latex exudation was only sampled at one point in time

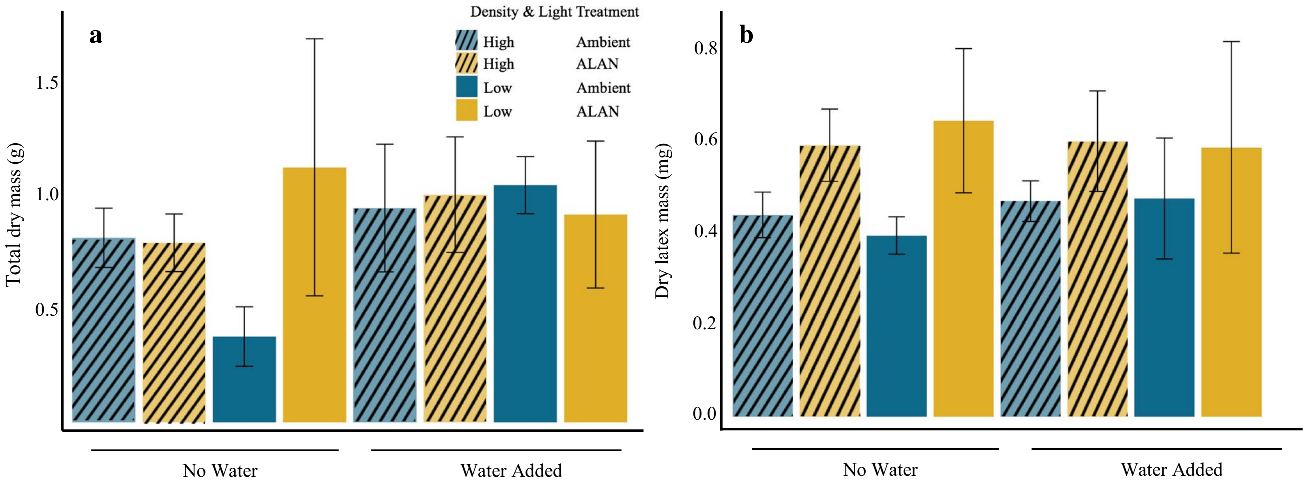

Fig. 2 Effects of artificial light at night (ALAN), plant density, and soil moisture on **a** total plant biomass (g) and **b** latex exudation (mg dry weight). Bars are means ± 1 SE

Table 4 Results of linear mixed-effects model on the effects of artificial light at night (ALAN), soil moisture, plant density, herbivore damage, and some two-way interactions on biomass (shoot + root mass, g) per plant

Source of variation	Estimate	SE	*df*	*t*	*p*
ALAN (*A*)	0.113	0.144	19.719	0.783	0.443
Soil moisture (S)	0.250	0.109	21.120	2.291	0.032*
Density (*D*)	−0.075	0.103	19.809	−0.727	0.476
Damage	−0.088	0.044	23.477	−2.002	0.057
A × *S*	−0.189	0.143	20.747	−1.324	0.200
A × *D*	0.217	0.145	19.941	1.498	0.150

*Significant at the *a* = 0.05 confidence level

**Significant at the *a* = 0.01 confidence level

***Significant at the *a* = 0.001 confidence level

(week 3), differences in the timing of the herbivory that occurred prior to our survey of latex production may also have inflated the variability in latex exudation as induced defenses in common milkweed have been shown to attenuate over time (Malcolm and Zalucki 1996).

Bennie et al. (2016) highlighted the need to explore interactions between ALAN and biotic interactions, including competition between plants. One mechanism whereby ALAN may affect competition in plants is promotion of vegetative growth. In some plant species, exposure to ALAN leads to increased vegetative growth (Cathey and Campbell 1975; Goins et al. 1998; Darko et al. 2014). Plants that exhibit increased stem elongation (increased height) in response to ALAN, as we observed for common milkweed (Fig. 1, Table 2), may gain a competitive advantage over plants in the absence of ALAN because the former would be less likely to become shaded by neighboring plants. Further research is needed to improve understanding of how ALAN interacts with the intra- and inter-specific competitive interactions of plants and to discern the key underlying mechanisms.

In our study, BSD responded more positively to ALAN in plants grown at low density than in plants grown at high density. This is consistent with our prediction that ALAN-induced increases in growth would be weaker in plants grown at the higher density because per-capita resource availability would decrease with increasing density. This interpretation would be more compelling if the same pattern was observed across multiple measures of plant growth, however, this finding suggests further study of interactions between ALAN and competition among plants is warranted. In light of previous research demonstrating that ALAN-induced changes in the growth and reproduction of vegetation can have bottom-up effects on consumers (Bennie et al. 2015; Grenis and Murphy 2019), it stands to reason that interactions between ALAN and competition among plants could plausibly influence food web structure.

Acknowledgements We would like to thank Brandon Fox and Dennis Heflin for the installing the experimental lighting infrastructure, Amoi Campbell for field assistance, and the staff of Blandy Experimental Farm for supporting original research in many ways.

Author contributions statement MH, KH, DR, DC, and ED conceived and designed the experiments. MH and ED performed the experiments. MH, DC, and KH analyzed the data. ED wrote the initial manuscript, which MH, DR, DC, and KH subsequently revised and edited.

Funding This study was funded by NSF REU Site Grants DBI 1156796 and DBI 1659816.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Agrawal AA, Fishbein M (2006) Plant defense syndromes. Ecology 87(sp7):S132–S149. https://doi.org/10.1890/0012-9658(2006)87[132:PDS]2.0.CO;2

Agrawal AA, Konno K (2009) Latex: a model for understanding mechanisms, ecology, and evolution of plant defense against herbivory. Annu Rev Ecol Evol Syst 40:311–331. https://doi.org/10.1146/annurev.ecolsys.110308.120307

Agrawal AA, Malcolm SB (2002) Once upon a milkweed—in this complex community, one insect's poison may be another's meal. Natural History September 2002

Agrawal AA, Patrick ET, Hastings AP (2014) Tests of the coupled expression of latex and cardenolide plant defense in common milkweed (*Asclepias syriaca*). Ecosphere 5:1–11. https://doi.org/10.1890/ES14-00161.1

Bates D, Mächler M, Bolker B, Walker S (2014) Fitting linear mixed-effects models using lme4. arXiv preprint arXiv:1406.5823

Bennie J, Davies TW, Cruse D, Inger R, Gaston KJ (2015) Cascading effects of artificial light at night: resource-mediated control of herbivores in a grassland ecosystem. Philos Trans R Soc B 370:20140131. https://doi.org/10.1098/rstb.2014.0131

Bennie J, Davies TW, Cruse D, Gaston KJ (2016) Ecological effects of artificial light at night on wild plants. J Ecol 104:611–620. https://doi.org/10.1111/1365-2745.12551

Bennie J, Davies TW, Cruse D, Bell F, Gaston KJ (2017) Artificial light at night alters grassland vegetation species composition and phenology. J Appl Ecol 55:442–450. https://doi.org/10.1111/1365-2664.12927

Bennie J, Davies TW, Cruse D, Inger R, Gaston KJ (2018) Artificial light at night causes top-down and bottom-up trophic effects on invertebrate populations. J Appl Ecol 55(6):2698–2706. https://doi.org/10.1111/1365-2664.13240

Briggs WR (2006) Physiology of plant responses to artificial lighting. In: Rich C, Longcore T (eds) Ecological consequences of artificial night lighting. Island Press, Washington DC, pp 389–406

Cathey HM, Campbell LE (1975) Security lighting and its impact on the landscape. J Arboric 1:181–187

Couture JJ, Serbin SP, Townsend PA (2015) Elevated temperature and periodic water stress alter growth and quality of common milkweed (*Asclepias syriaca*) and monarch (*Danaus plexippus*) larval performance. Arthropod-Plant Interact 9:149–161. https://doi.org/10.1007/s11829-015-9367-y

Darko E, Heydarizadeh P, Schoefs B, Sabzalian MR (2014) Photosynthesis under artificial light: the shift in primary and secondary metabolism. Philos Trans R Soc B Biol Sci 369(1640):20130243. https://doi.org/10.1098/rstb.2013.0243

Davies TW, Bennie J, Gaston KJ (2012) Street lighting changes the composition of invertebrate communities. Biol Lett 8(5):764–767. https://doi.org/10.1098/rsbl.2012.0216

Davies TW, Bennie J, Cruse D et al (2017) Multiple night-time light-emitting diode lighting strategies impact grassland invertebrate assemblages. Glob Chang Biol 23:2641–2648. https://doi.org/10.1111/gcb.13615

Falchi F, Cinzano P, Duriscoe D, Kyba CC, Elvidge CD, Baugh K et al (2016) The new world atlas of artificial night sky brightness. Sci Adv 2(6):e1600377. https://doi.org/10.1126/sciadv.1600377

Farnworth B, Innes J, Kelly C, Littler R, Waas JR (2018) Photons and foraging: artificial light at night generates avoidance behaviour in male, but not female, New Zealand weta. Environ Pollut 236:82–90. https://doi.org/10.1016/j.envpol.2018.01.039

Firebaugh A, Haynes KJ (2019) Light pollution may create demographic traps for nocturnal insects. Basic Appl Ecol 34:118–125. https://doi.org/10.1016/j.baae.2018.07.005

Gaston KJ, Bennie J, Davies TW, Hopkins J (2013) The ecological impacts of nighttime light pollution: a mechanistic appraisal. Biol Rev 88:912–927. https://doi.org/10.1111/brv.12036

Goins GD, Yorio NC, Sanwo-Lewandowski MM, Brown CS (1998) Life cycle experiments with Arabidopsis under red light-emitting diodes (LEDs). Life Support Biosph Sci 5:143–149

Greenham K, McClung CR (2015) Integrating circadian dynamics with physiological processes in plants. Nat Rev Genet 16:598–610. https://doi.org/10.1038/nrg3976

Grenis K, Murphy SM (2019) Direct and indirect effects of light pollution on the performance of an herbivorous insect. Insect Sci 26:770–776. https://doi.org/10.1111/1744-7917.12574

Guo Y, Logan HL, Glueck DH, Muller KE (2013) Selecting a sample size for studies with repeated measures. BMC Med Res Methodol 13(1):100. https://doi.org/10.1186/1471-2288-13-100

Huot B, Yao J, Montgomery BL, He SY (2014) Growth-defense tradeoffs in plants: a balancing act to optimize fitness. Mol Plant 7:1267–1287. https://doi.org/10.1093/mp/ssu049

Jin X, Li Y, Zhang J, Zheng J, Liu H (2017) An approach to evaluating light pollution in residential zones: a case study of Beijing. Sustainability 9(4):652

Knop E, Zoller L, Ryser R et al (2017) Artificial light at night as a new threat to pollination. Nature 548:206–209. https://doi.org/10.1038/nature23288

Kuznetsova A, Brockhoff PB, Christensen RH (2017) lmerTest package: tests in linear mixed effects models. J Stat Softw 82(13):3–12

Kwak MJ, Lee SH, Khaine I, Je SM, Lee TY, You HN, Lee HK, Jang JH, Kim I, Woo SY (2017) Stomatal movements depend on interactions between external night light cue and internal signals activated by rhythmic starch turnover and abscisic acid (ABA) levels at dawn and dusk. Acta Physiol Plant 39(8):162

Kwak MJ, Je SM, Cheng HC, Seo SM, Park JH, Baek SG, Khaine I, Lee T, Jang J, Li Y, Kim H (2018) Night light-adaptation strategies for photosynthetic apparatus in yellow-poplar (*Liriodendron tulipifera* L.) exposed to artificial night lighting. Forests 9(2):74. https://doi.org/10.3390/f9020074

Lawson T, Blatt MR (2014) Stomatal size, speed, and responsiveness impact on photosynthesis and water use efficiency. Plant Physiol 164(4):1556–1570. https://doi.org/10.1104/pp.114.237107

Lind EM, Borer E, Seabloom E et al (2013) Life-history constraints in grassland plant species: a growth-defence trade-off is the norm. Ecol Lett 16:513–521. https://doi.org/10.1111/ele.12078

Longcore T, Rich C (2004) Ecological light pollution. Front Ecol Environ 2:191–198. https://doi.org/10.1890/1540-9295(2004)002[0191:ELP]2.0.CO;2

Macgregor CJ, Evans DM, Fox R, Pocock MJO (2017) The dark side of street lighting: impacts on moths and evidence for the disruption of nocturnal pollen transport. Glob Chang Biol 23:697–707. https://doi.org/10.1111/gcb.13371

Malcolm SB, Zalucki MP (1996) Milkweed latex and cardenolide induction may resolve the lethal plant defence paradox. In: Proceedings of the 9th international symposium on insect-plant relationships, pp 193–196

Nichter A, Gregory A (2018) Distribution modeling of *Asclepias* spp. predicts potential conservation benefits of marginal ecosystems as nature reserves in Northwest Ohio. Nat Areas J 38(4):250–259. https://doi.org/10.3375/043.038.0405

R Core Team (2019) R: a language and environment for statistical 1031 computing. Vienna, Austria: R Foundation for Statistical Computing 1032

Robertson FC, Skeffington AW, Gardner MJ, Webb AA (2009) Interactions between circadian and hormonal signaling in plants. Plant Mol Biol 69(4):419. https://doi.org/10.1007/s11103-008-9407-4

Sanders D, Kehoe R, Tiley K et al (2015) Artificial nighttime light changes aphid-parasitoid population dynamics. Sci Rep 5:15232. https://doi.org/10.1038/srep15232

Van Zandt PA, Agrawal AA (2004) Specificity of induced plant responses to specialist herbivores of the common milkweed Asclepias syriaca. Oikos 104(2):401–409. https://doi.org/10.1111/j.0030-1299.2004.12964.x

Witherington BE, Martin RE (2000) Understanding, assessing, and resolving light-pollution problems on sea turtle nesting beaches. Florida Marine Research Institute. Technical Report TR-2

Züst T, Agrawal AA (2017) Trade-offs between plant growth and defense against insect herbivory: an emerging mechanistic synthesis. Annu Rev Plant Biol 68:513–534. https://doi.org/10.1146/annurev-arplant-042916-040856