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Effects of Low-Level Artificial Light at Night on Kentucky Bluegrass and Introduced Herbivore

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Abstract

Increasing evidence suggests that artificial light at night (ALAN) can negatively impact organisms. However, most studies examine the impacts of ALAN on a single species or under high levels of artificial light that are infrequent or unrealistic in urban environments. We currently have little information on how low levels of artificial light emanating from urban skyglow affect plants and their interactions with herbivores. We examined how low levels of ALAN affect grass and insects, including growth rate, photosynthesis, and stomatal conductance in grass, and foraging behavior and survival in crickets. We compared growth and leaf-level gas exchange of Kentucky Bluegrass (*Poa pratensis*) under low-levels of ALAN (0.3 lux) and starlight conditions (night light at 0.001 lux). Furthermore, each light treatment was divided into treatments with and without house crickets (*Acheta domesticus*). Without crickets present, bluegrass grown under artificial light at night for three weeks grew taller than plants grown under natural night light levels. Once crickets were introduced at the end of week three, grass height decreased resulting in no measurable effects of light treatment. There were no measurable differences in grass physiology among treatments. Our results indicate that low levels of light resulting from skyglow affect plant growth initially. However, with herbivory, ALAN effects on grass may be inconsequential. Gaining an understanding of how ALAN effects plant-insect interactions is critical to predicting ecological and evolutionary consequences of anthropogenic disturbance.

1 Introduction

Artificial light at night (ALAN) is an anthropogenic pollutant that is increasing spatially by a rate of 2.2% per year (Kyba et al., 2017). Direct ALAN sources, such as streetlights, can lead to skyglow: the atmospheric scattered light that can propagate up to several hundred kilometers into the environment (Aubé, 2015; Luginbuhl et al., 2009; Aubé, 2015). Skyglow results in light encroaching into natural areas where direct sources of light pollution are not present (Gaston et al., 2015; Garrett et al., 2020). The study of artificial light at night as an anthropogenic pollutant is a relatively young field (Longcore and Rich, 2004; Seymoure, 2018; Dominoni et al., 2020; Sanders et al., 2021), with most studies conducted at relatively high levels of nocturnal light pollution (e.g., 10-100 lux; (Gaston et al., 2013) but see (Alaasam et al., 2018; Sanders and Gaston, 2018). These high light levels are representative of organisms functioning under direct light pollution, such as directly beneath a streetlight, whereas most urban environments exist at lower light levels due to skyglow (e.g., 0.1 to 1 lux), which can impact environments several hundred kilometers away from a direct light source (Gaston et al., 2013; Dominoni et al., 2014; Seymoure et al., 2019a). For reference, a full moon night could create ambient light levels of 0.3 lux on its brightest nights (Biberman et al., 1966; Kyba et al., 2017). Therefore, examining the impacts of light pollution at high intensities, although informative, is not representative of artificial light conditions in urban habitats at night. It remains an open question as to whether low levels of skyglow illumination (0.001 lux - 0.3 lux) affects communities to the same extent as direct illumination.

The intensity and spectral composition of light depends upon the phase of the moon, season, and weather, all of which create necessary cues for organisms (Kyba et al., 2015; Spitschan et al., 2016; Seymoure et al., 2019b). Plants use light as a cue for almost every physiological process including, but not limited to, seedling development, photosynthesis, growth, and budding (Takemiya et al., 2005; Bennie et al., 2016; Gaston et al., 2017; Singhal et al., 2018). Light influences plant growth, development, and photosynthetic efficiency (Briggs and Christie, 2002). In addition to powering the electron transport chain in thylakoid membranes, light intensity and direction increases photosynthetic efficiency through phototropism (i.e. the movement of the plant towards sunlight; (Celaya and Liscum, 2005), chloroplast movement (Wada et al., 2003), and light-induced stomatal opening to help optimize gas exchange efficiency (Dietrich et al., 2001). Periods of darkness are also important for plant metabolic processes, particularly stress recovery, which includes recovery from herbivory events (McNaughton, 1983; Singhal et al., 2018).

Increased levels of ALAN from urbanization are changing natural light regimes by increasing the intensity and duration of light available at night (Davies et al., 2013; Seymoure et al., 2019a; Buxton et al., 2020), potentially affecting plant photosynthesis, growth, and plant-herbivore interactions. For example, by masking natural night light levels, ALAN can mislead herbivores to be more active at night and disrupt plant-herbivore interactions and critical dark recovery periods for plants (Dominoni et al., 2020). Plants in light polluted environments experience changes in pollination, photoreceptor signaling, phenology and flowering (Ffrench-Constant et al., 2016; Singhal et al., 2018), which can have ecological consequences for food web dynamics (Polis et al., 2004). However, little is known about how constant illumination at the level of urban light alters plant-insect interactions. ALAN has led to declines in population sizes of a diversity of insect species through its interference with insect development, movement, foraging, and reproductive success, which can alter trophic systems (Owens and Lewis, 2018; Owens et al., 2020).

Here we test whether ALAN affects plant-insect interactions by modifying plant photobiology and growth rates. We exposed two common urban species—Kentucky bluegrass (*Poa pratensis*), a cool season common turfgrass (Weissman et al., 1977; Suplick-Ploense and Qian, 2005; Read et al., 1999; Weissman et al., 1977; Suplick-Ploense and Qian, 2005), and the house cricket

(*Acheta domesticus*), a nocturnal herbivore—to starlight (0.001 lux) and realistic urban night light levels (0.3 lux) (Dominoni et al., 2013; Alaasam et al., 2018; Seymoure et al., 2019a) in order to test the following hypotheses: 1) Low levels of ALAN affect plant physiology. We predicted that plants grown under urban light would have higher net photosynthesis and dark respiration, increased growth rates, and increased stomatal conductance compared to control plants grown under starlight conditions. 2) Herbivory interacts with ALAN to affect plant biomass. We predicted cricket herbivores would reduce the biomass and height of grass. However, as crickets are nocturnal foragers, we predicted they would consume less plant material under urban light than starlight conditions and have lower survival rates in urban light.

2 Materials and Methods

2.1 Light Treatments

We used a CMP6050 growth chamber (Version 4.06, Conviron, Winnipeg, Manitoba) set to a temperature of 22.2°C with light control to create artificial light environments (0.3 lux, hereafter "urban light") and natural new moon light environments (0.001 lux, hereafter "starlight")(Dominoni et al., 2013; Alaasam et al., 2018; Seymoure et al., 2019a; Jones et al., 2020). There were two different light types in the chamber - high pressure sodium and mercury vapor - placed in alternating positions on the ceiling of the chamber. To create urban light levels within the chamber, we used 4 layers of filter gels over the light sources (Rosco E-Colour #211 .9 Neutral Density Filter, Stamford, CT) that attenuated 83% of light. To further attenuate light, 90% black shade cloth was placed over starlight treatments, and 22% white shade cloth was placed over urban light environments. These were constructed as square boxes and placed over the plant treatment groups using PVC pipe and shade cloth. We confirmed that light levels were approximately 0.3 lux and 0.001 lux using a highly sensitive spectroradiometer (StellarNet Silver Nova, Tampa Bay, FL) with a cosine corrected irradiance probe affixed to a 1000-micron optical fiber (StellarNet, Tampa Bay, FL). We checked irradiance measurements using SpectraWhiz software (StellarNet, Tampa Bay, FL); due to the low light levels, we set integration time to approximately 20 seconds for the 0.3 lux measurements and 8 minutes for the 0.001 lux measurements. This confirmed that light levels throughout the enclosure were within one order of magnitude of the chosen light level for each treatment: 0.3 and 0.001 lux.

2.2 Experimental Design

On day 1, Kentucky bluegrass seeds were sown in 10 cm round pots (n=72) containing Scotts Miracle-Gro soil and placed in the growth chamber under experimental light conditions. On day 21, we measured the tallest blade of grass, then weeded down the pots randomly until there were 25 shoots of grass remaining. After the initial 21-day growth period, one randomly selected juvenile cricket, male or female, was placed in each of 36 designated cricket pots. Herbivory and light environments were examined using a 2x2 factorial design in which light treatment was factorially crossed with cricket treatment in a 28-day experiment. The four treatments were arranged in a block test pattern, as shown in **Figure 1**. Treatment groups included: (1) plants without crickets in urban light, (2) plants without crickets in starlight, (3) plants with crickets in urban light, and (4) plants with crickets in starlight (n=18 per treatment). Nighttime lighting conditions were imposed in the middle of the day from start of the experiment to ensure nighttime measurements could be taken during regular working hours. Lighting conditions were altered twice daily; we placed filter paper and shade cloth structures over the plants at 08:00 and removed them at 18:00 to create a 14:10 light: dark cycle typical of summer in the northern hemisphere. Blocks were rotated daily one position clockwise to account for spatial variation in light levels within the chamber, and generously watered at this time.

Drierite (W.A. Hammond 23005, Xenia, OH) was placed in two trays on opposite sides of the chamber to control humidity and prevent mold growth (Hammond, 1935).

Crickets were sourced as juveniles from a stock population from Premium Crickets (Winder, Georgia) in December 2018 and May 2019 at the mean size of 1.9 centimeters, before adult morph. From day 21 to 28, cricket survival was monitored daily (i.e., when light conditions were shifted) and categorized as alive or dead. If a cricket was found dead, the cricket and its designated plant were removed from the experiment. Upon removal, we measured the height of the tallest blade of grass and recorded the length of time the plant/cricket spent in the chamber. We also cut and weighed above ground biomass to determine wet and dry mass. On day 28, we removed all remaining plants from the experiment and recorded the final height of the tallest blade of grass. We calculated the average daily growth rate in week four (day 21 to day 28) to control for plants that were removed prematurely due to cricket death.

2.3 Gas Exchange Measurements

To assess light treatment effects on bluegrass physiology independent of herbivory, we measured leaf photosynthetic responses on day 19 before crickets were placed into pots. We measured leaf gas exchange in each light treatment using a LI-6400XT infrared gas analyzer with a leaf chamber fluorometer attached (Li-Cor Biosciences; Lincoln, NE) following previously published methods with slight modifications (Lemoine et al., 2018). Plants were removed from the growth chamber temporarily for gas exchange measurements. The environmental conditions inside the leaf chamber were standardized across measurements; leaf temperature was maintained at 20°C, relative humidity was maintained between 40-50%, sample chamber flow rate was set to 200 μmol s^{-1}, and reference chamber CO_2 concentration was set to 400 ppm. Low flow settings are commonly used for small leaved grasses with low photosynthetic rates (Taylor, 2014). Leaf level gas exchange was measured under two light conditions: dark and low light (10 μmol m^2 s^{-1} (740 lx) photosynthetically active radiation; PAR). Gas exchange in the dark provides an estimation of leaf respiration. The low light level was the minimum amount of light provided by the Li-6400 light source; thus, we were unable to measure photosynthesis under the tested ALAN conditions imposed here (<10 umols, <740 lux), but instead measured whether treatments had an impact on plant photosynthetic responses to low levels of light. Results are reported in regard to light treatment in the growth chamber (urban light or starlight). A newly emerged and fully expanded leaf from each individual (n= 10 individuals per treatment) was inserted into the leaf chamber. Prior to measurements, leaves were dark adapted for 2 hours under a dark box that allowed no light to enter. Leaves were left in the chamber for 2-5 minutes to equilibrate to chamber conditions before gas exchange parameters (photosynthesis or respiration, and stomatal conductance) were recorded (average of three logged values taken in rapid succession). Steady-state fluorescence (Fs) was measured continuously before exposing plants to a saturating pulse of light (2750 μmol m^{-2} s^{-1} of blue light or ~203,500 lux (Thimijan and Heins, 1983) to measure maximum chlorophyll fluorescence. Light inside the chamber was then switched to the low light level (10 μmol m^2 s^{-1}). Once gas exchange reached stability, net photosynthetic rate, and stomatal conductance were recorded, and a saturating pulse was applied to estimate photosystem II efficiency (ΦPSII): $\Phi PSII = (Fm' - Fs)/Fm'$ where Fm' represents chlorophyll fluorescence under low light. As grass blades rarely fill the entire chamber, the measured leaf area was estimated using width and length, and photosynthetic parameters, which are based on the area of the chamber (6 cm^2), were adjusted accordingly.

2.4 Data Analysis

All statistical analyses were performed in R version 3.4.3(R Development Core Team, 1999). We first confirmed the use of parametric tests to ensure our data was normally distributed. To test our first hypothesis that gas exchange increased under ALAN, we ran a MANOVA with net photosynthetic rate, stomatal conductance, dark respiration, and ΦPSII as response variables and with light treatment and block as explanatory variables (**Figure 2**). For our second hypothesis that light and cricket treatments would affect plant height, we modeled daily percent change in height between day 21 and day 28 using a two-way ANOVA with light treatment, cricket treatment, and block as explanatory variables (**Figure 3**). We then analyzed the data using two-way ANOVA, again with light treatment, cricket treatment, and block as explanatory variables. We tested for an interaction between light treatment and cricket treatment, and we also analyzed cricket survival using Kaplan-Meier analysis with the "survival" package in R (**Figure 4**) (Therneau and Lumley, 2009).

3 Results

There was no difference in net photosynthesis, stomatal conductance, dark respiration, or ΦPSII between grass grown in the two light treatments (**Table 1**). On day 21, bluegrass grown in urban light was taller (mean = 6.58cm, sd = 2.3) than bluegrass grown in starlight (mean = 7.10cm, sd = 2.67, **Table 2**). However, daily percent change in plant height from day 21 to day 28 was not significantly different (**Table 3**). The presence of crickets did affect plant height, whereby bluegrass with crickets present were shorter than bluegrass without crickets (**Table 3**).
Crickets in the urban light treatment had a 25.0% probability of survival, whereas crickets in the starlight treatment had a survival probability of 32.1%, but this difference was not significant (Kaplan-Meier: n = 36, p = 0.37, see supplemental material). There was no difference in survival due to sex (Kaplan-Meier: n= 36, p= 0.80, see supplemental material).

4 Discussion

Our study explored how low levels of artificial light at night, which are widespread across ecosystems, may affect plants and plant-insect interactions. Contrary to our predictions, grass grown under urban light conditions after 19 days did not have higher net photosynthetic rates than those grown under starlight, nor did stomatal conductance, dark respiration, or ΦPSII differ significantly between light treatments. However, plants under urban light conditions grew taller than plants grown under starlight conditions during the initial 21 days of growth before crickets were introduced. Additionally, we found no evidence that crickets under urban light consumed more plant matter than crickets in starlight treatments, and survival rates of crickets did not differ between treatments. The results from this study suggest that low levels of ALAN may not have significant effects on grass photobiology but may affect plant height.

Studies investigating grass responses to higher levels of illumination (e.g., 4±1 μmol?m-2?s-1 or 296 lux) found that plant photoreceptors were damaged causing changes to flowering phenology (Thimijan and Heins, 1983; Shin et al., 2010; Bennie et al., 2016). The lower levels of light tested here were likely not bright enough to induce these changes in bluegrass. Plants often use nighttime darkness to repair damage from UV rays, suggesting the low levels of ALAN in our treatments may be dark enough for plants to continue to repair damaged cells and photoreceptors (Singhal et al., 2018). Moreover, net photosynthesis is a dynamic measurement that can vary within samples due to time and day(Miller et al., 1996) and our single measurement at the end of week 3 may not have captured treatment differences occurring at other times.

We found no difference in stomatal conductance or respiration between plants grown in urban light and starlight. Other studies have noted differences in stomatal density and stomatal opening and closing in the presence of ALAN (Takemiya et al., 2005; Shimazaki et al., 2007). Another study found that yellow-poplar trees exposed to ALAN (high pressure sodium lighting ranging from 82 lx to 4100 lx) for three years resulted in reduced nighttime stomatal conductance (Kwak et al., 2018). It is possible that our light levels were too low, or grass was not subjected to our light levels for a long enough duration to induce such responses. Reduced chlorophyll and rubisco concentration has been observed in phytoplankton grown under low light levels (6.6 lux;(Poulin et al., 2014), and light as low as 3.5 lux has induced flowering in tree species across the United Kingdom (Ffrench-Constant et al., 2016). We also observed no treatment effects on photosystem II efficiency despite other studies noting adverse reactions in these physiological responses to light pollution (Zhang and Reisner, 2019; Meravi and Prajapati, 2020). Kentucky Bluegrass might be more adaptable to changing light regimes given that it is commonly used as a turf grass selected for its resilience to drought and heat stress (Wang and Huang, 2004). We observed a faster growth rate for grasses grown under urban light conditions compared to starlight conditions. Plant growth rate is determined by a variety of factors, including, but not limited to, photosynthetic rate, specific leaf area, leaf mass fraction, and nitrogen absorption rate(Poorter et al., 1991; Osone et al., 2008). Although we found no difference in net photosynthetic rate between treatments, growth rate differences could have been due to greater allocation to leaf area in urban light(Poorter and Remkes, 1990), although we did not measure such attributes.

ALAN is known to alter photoperiod detection in multiple organisms (Bennie et al., 2016) and these changes in photoperiod can impact plant growth and flowering (Cathey and Campbell, 1975; Blanchard and Runkle, 2010; Basler and Körner, 2012; Craig and Runkle, 2016). Increased growth and biomass have been noted in *Poaceae* species when exposed to high levels of ALAN ranging from 0.349 - 1.145μmols m^2 sec^{-1} from metal halide bulbs (Flowers and Gibson, 2018), which is approximately 24.78 - 81.30 lux (Thimijan and Heins, 1983). Since we noted no change in Kentucky Bluegrass, photoperiod detection may not have been disrupted at our lower levels of ALAN, or it may have caused undetectable or non-measured physiological responses.

While animals rely on plants as a food source and shelter, we found no evidence that low-level light pollution would impact these typical interactions between plants and insects. Artificial light at the level of 0.3 lux was not significant enough to mask natural light cues in herbivores, nor mislead herbivores in foraging behaviors, but light pollution at higher levels could modify these interactions(Gaston et al., 2013; Macgregor et al., 2015; Bennie et al., 2016; Knop et al., 2017). High levels of ALAN could mask lunar cues, disrupting invertebrate behavior and feeding patterns and could attract invertebrates to artificially lit structures, deterring them from normal behavioral patterns (Longcore and Rich, 2004; Seymoure, 2018; Dominoni et al., 2020; Sanders et al., 2021).

Overall, our research detected few changes to plant physiology at low levels of urban light, suggesting that low levels of ALAN may not be as harmful to community interactions as predicted. Other studies conducted at high levels of ALAN suggest artificial light can induce large changes in physiology and community interactions(Longcore and Rich, 2004; Gaston et al., 2013; Seymoure et al., 2019a). There may be a threshold level at which artificial light becomes harmful, causing detrimental effects to individual and ecosystem function with additional increases in intensity and duration. Understanding and identifying this threshold would allow for more effective management of night skies and natural light conditions(Dominoni et al., 2020). With estimates suggesting two thirds of Key Biodiversity Areas experience ALAN(Seymoure et al., 2019a; Garrett et al., 2020), it is

important to identify the level at which artificial light becomes harmful and how natural night skies can be managed.

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The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Table 1 MANOVA table of the gas exchange results evaluating differences in photosynthesis, stomatal conductance in dark, stomatal conductance in light, fluorescence, and photosystem II efficiency.

	df	Pillai	*f*	*p*
Treatment	**1**	**0.18**	**0.45**	**0.83**
Block	**3**	**0.95**	**1.09**	**0.40**
Residuals	**17**			

Table 2 ANOVA table comparing mean grass height at day 21 across light treatments and blocks. * indicates a significant response.

	Sum of Squares	*df*	Mean Square	F	*p*
Light Treatment	**3.50**	**1**	**3.50**	**5.63**	**0.021***
Block	**7.87**	**6**	**1.31**	**2.11**	**0.064**
Residuals	**39.8**	**64**	**0.622**		

Table 3 ANOVA table showing the effects of light treatment, cricket treatment, and block (plus interactions between light and cricket treatment and cricket and block treatment) on daily percent change in grass height between day 21 and the end of the experiment. * indicates a significant response.

	Sum of Squares	*df*	Mean Square	F	*p*
Light Treatment	**0.14**	**1**	**0.14**	**1.60**	**0.21**
Cricket Treatment	**2.82**	**1**	**2.82**	**32.04**	**5.3×10^{-7}***
Block	**0.85**	**6**	**0.14**	**1.62**	**0.16**
Light: Cricket	**0.002**	**1**	**0.002**	**0.023**	**0.88**
Cricket: Block	**0.90**	**6**	**0.15**	**1.70**	**0.14**
Residuals	**4.93**	**56**	**0.088**		

Figure 1: Aerial view of treatment groups in the growth chamber after crickets were introduced (day 21-28). The treatment groups were arranged in a block test pattern with 4 blocks of urban light treatments and 4 blocks of starlight treatments, totaling 8 groups (A-H). Within each block (A-H), nine plants (every other one) had a cricket.

Figure 2: (A) Net photosynthesis across light treatments, measured under low light conditions (10 μmols m^{-2} s^{-1} of light) and **(B)** stomatal conductance across light treatments. **(C)** Photosystem II efficiency is measured using a saturating pulse (ΦPSII): ΦPSII = (Fm′ − Fs)/Fm' where Fm is chlorophyll fluorescence under low light. **(D)** Dark respiration measured under low light level (<10 μmols m^{-2} s^{-1} of light). There were no differences in net photosynthesis, stomatal conductance, Photosystem II efficiency, or dark respiration between light treatments.

Figure 3: (A) Bluegrass height at day 21 separated by light treatment when no crickets were present. Grass in urban light was taller than grass in starlight conditions. **(B)** Daily percent change in height of grass (change from day 21 to day 28 divided by the number of days in the chamber) separated by light treatment. There was no difference in daily percent change across light or cricket treatments.

Figure 4: Survival probability of crickets. **(A)** Survival probability of crickets under urban light and starlight treatments. **(B)** Survival probability of crickets under urban light and starlight treatments, split by sex in each treatment group. In all both comparisons **(A-B)**, there were no differences in survival.