1. Word Count: 3,163
2. Tables: 3
3. Figures: 4
4. **Effects of low-level artificial light at night on Kentucky bluegrass and**
5. **introduced herbivore**
6. **Running Title:** Artificial light at night effects on bluegrass and herbivore 7

# Morgan Crump1,2†, Cassandra Brown1,2†, Robert J. Griffin-Nolan2,3, Lisa Angeloni2, Nathan P.

1. **Lemoine4, and Brett Seymoure1,2,5\***

10

11 †These authors have contributed equally to this work and share first authorship 12

1. 1 Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort
2. Collins, CO, 80523
3. 2 Department of Biology, Colorado State University, Fort Collins, CO, 80523
4. 3 Department of Biology, Syracuse University, Syracuse, NY, 13244
5. 4 Department of Biological Science, Marquette University, Milwaukee, WI, 53201 and Department
6. of Zoology, Milwaukee Public Museum, Milwaukee, WI, 53201
7. 5 Living Earth Collaborative, Washington University in St. Louis, St. Louis, MO, 63130 20

# \* Correspondence:

1. Dr. Brett Seymoure
2. [brett.seymoure@gmail.com](mailto:brett.seymoure@gmail.com)

# Keywords: photosynthesis, urban light, crickets, insects, growth rate.

1. **Abstract**
2. Increasing evidence suggests that artificial light at night (ALAN) can negatively impact
3. organisms. However, most studies examine the impacts of ALAN on a single species or under high
4. levels of artificial light that are infrequent or unrealistic in urban environments. We currently have
5. little information on how low levels of artificial light emanating from urban skyglow affect plants
6. and their interactions with herbivores. We examined how low levels of ALAN affect grass and
7. insects, including growth rate, photosynthesis, and stomatal conductance in grass, and foraging
8. behavior and survival in crickets. We compared growth and leaf-level gas exchange of Kentucky
9. Bluegrass (*Poa pratensis*) under low-levels of ALAN (0.3 lux) and starlight conditions (night light at
10. 0.001 lux). Furthermore, each light treatment was divided into treatments with and without house
11. crickets (*Acheta domesticus*). Without crickets present, bluegrass grown under artificial light at night
12. for three weeks grew taller than plants grown under natural night light levels. Once crickets were
13. introduced at the end of week three, grass height decreased resulting in no measurable effects of light
14. treatment. There were no measurable differences in grass physiology among treatments. Our results
15. indicate that low levels of light resulting from skyglow affect plant growth initially. However, with
16. herbivory, ALAN effects on grass may be inconsequential. Gaining an understanding of how ALAN
17. effects plant-insect interactions is critical to predicting ecological and evolutionary consequences of
18. anthropogenic disturbance.

# 1 Introduction

1. Artificial light at night (ALAN) is an anthropogenic pollutant that is increasing spatially by a
2. rate of 2.2% per year (Kyba et al., 2017). Direct ALAN sources, such as streetlights, can lead to
3. skyglow: the atmospheric scattered light that can propagate up to several hundred kilometers into the
4. environment (Aubé, 2015; Luginbuhl et al., 2009; Aubé, 2015). Skyglow results in light encroaching
5. into natural areas where direct sources of light pollution are not present (Gaston et al., 2015; Garrett
6. et al., 2020). The study of artificial light at night as an anthropogenic pollutant is a relatively young
7. field (Longcore and Rich, 2004; Seymoure, 2018; Dominoni et al., 2020; Sanders et al., 2021), with
8. most studies conducted at relatively high levels of nocturnal light pollution (e.g., 10-100 lux; (Gaston
9. et al., 2013) but see (Alaasam et al., 2018; Sanders and Gaston, 2018). These high light levels are
10. representative of organisms functioning under direct light pollution, such as directly beneath a
11. streetlight, whereas most urban environments exist at lower light levels due to skyglow (e.g., 0.1 to 1
12. lux), which can impact environments several hundred kilometers away from a direct light source
13. (Gaston et al., 2013; Dominoni et al., 2014; Seymoure et al., 2019a). For reference, a full moon night
14. could create ambient light levels of 0.3 lux on its brightest nights (Biberman et al., 1966; Kyba et al.,
15. 2017). Therefore, examining the impacts of light pollution at high intensities, although informative,
16. is not representative of artificial light conditions in urban habitats at night. It remains an open
17. question as to whether low levels of skyglow illumination (0.001 lux - 0.3 lux) affects communities
18. to the same extent as direct illumination.
19. The intensity and spectral composition of light depends upon the phase of the moon, season,
20. and weather, all of which create necessary cues for organisms (Kyba et al., 2015; Spitschan et al.,
21. 2016; Seymoure et al., 2019b). Plants use light as a cue for almost every physiological process
22. including, but not limited to, seedling development, photosynthesis, growth, and budding (Takemiya
23. et al., 2005; Bennie et al., 2016; Gaston et al., 2017; Singhal et al., 2018). Light influences plant
24. growth, development, and photosynthetic efficiency (Briggs and Christie, 2002). In addition to
25. powering the electron transport chain in thylakoid membranes, light intensity and direction increases
26. photosynthetic efficiency through phototropism (i.e. the movement of the plant towards sunlight;
27. (Celaya and Liscum, 2005), chloroplast movement (Wada et al., 2003), and light-induced stomatal
28. opening to help optimize gas exchange efficiency (Dietrich et al., 2001). Periods of darkness are also
29. important for plant metabolic processes, particularly stress recovery, which includes recovery from
30. herbivory events (McNaughton, 1983; Singhal et al., 2018).
31. Increased levels of ALAN from urbanization are changing natural light regimes by increasing
32. the intensity and duration of light available at night (Davies et al., 2013; Seymoure et al., 2019a;
33. Buxton et al., 2020), potentially affecting plant photosynthesis, growth, and plant-herbivore
34. interactions. For example, by masking natural night light levels, ALAN can mislead herbivores to be
35. more active at night and disrupt plant-herbivore interactions and critical dark recovery periods for
36. plants (Dominoni et al., 2020). Plants in light polluted environments experience changes in
37. pollination, photoreceptor signaling, phenology and flowering (Ffrench-Constant et al., 2016; Singhal
38. et al., 2018), which can have ecological consequences for food web dynamics (Polis et al., 2004).
39. However, little is known about how constant illumination at the level of urban light alters plant-insect
40. interactions. ALAN has led to declines in population sizes of a diversity of insect species through its
41. interference with insect development, movement, foraging, and reproductive success, which can alter
42. trophic systems (Owens and Lewis, 2018; Owens et al., 2020).
43. Here we test whether ALAN affects plant-insect interactions by modifying plant
44. photobiology and growth rates. We exposed two common urban species—Kentucky bluegrass (*Poa*
45. *pratensis*), a cool season common turfgrass (Weissman et al., 1977; Suplick-Ploense and Qian, 2005;
46. Read et al., 1999; Weissman et al., 1977; Suplick-Ploense and Qian, 2005), and the house cricket
47. (*Acheta domesticus*), a nocturnal herbivore—to starlight (0.001 lux) and realistic urban night light
48. levels (0.3 lux) (Dominoni et al., 2013; Alaasam et al., 2018; Seymoure et al., 2019a) in order to test
49. the following hypotheses: 1) Low levels of ALAN affect plant physiology. We predicted that plants
50. grown under urban light would have higher net photosynthesis and dark respiration, increased growth
51. rates, and increased stomatal conductance compared to control plants grown under starlight
52. conditions. 2) Herbivory interacts with ALAN to affect plant biomass. We predicted cricket
53. herbivores would reduce the biomass and height of grass. However, as crickets are nocturnal
54. foragers, we predicted they would consume less plant material under urban light than starlight
55. conditions and have lower survival rates in urban light.

# 2 Materials and Methods

## 2.1 Light Treatments

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

## 2.2 Experimental Design

1. On day 1, Kentucky bluegrass seeds were sown in 10 cm round pots (n=72) containing Scotts
2. Miracle-Gro soil and placed in the growth chamber under experimental light conditions. On day 21,
3. we measured the tallest blade of grass, then weeded down the pots randomly until there were 25
4. shoots of grass remaining. After the initial 21-day growth period, one randomly selected juvenile
5. cricket, male or female, was placed in each of 36 designated cricket pots. Herbivory and light
6. environments were examined using a 2x2 factorial design in which light treatment was factorially
7. crossed with cricket treatment in a 28-day experiment. The four treatments were arranged in a block
8. test pattern, as shown in **Figure 1**. Treatment groups included: (1) plants without crickets in urban
9. light, (2) plants without crickets in starlight, (3) plants with crickets in urban light, and (4) plants with
10. crickets in starlight (n=18 per treatment). Nighttime lighting conditions were imposed in the middle
11. of the day from start of the experiment to ensure nighttime measurements could be taken during
12. regular working hours. Lighting conditions were altered twice daily; we placed filter paper and shade
13. cloth structures over the plants at 08:00 and removed them at 18:00 to create a 14:10 light: dark cycle
14. typical of summer in the northern hemisphere. Blocks were rotated daily one position clockwise to
15. account for spatial variation in light levels within the chamber, and generously watered at this time.
16. Drierite (W.A. Hammond 23005, Xenia, OH) was placed in two trays on opposite sides of the
17. chamber to control humidity and prevent mold growth (Hammond, 1935).
18. Crickets were sourced as juveniles from a stock population from Premium Crickets (Winder,
19. Georgia) in December 2018 and May 2019 at the mean size of 1.9 centimeters, before adult morph.
20. From day 21 to 28, cricket survival was monitored daily (i.e., when light conditions were shifted) and
21. categorized as alive or dead. If a cricket was found dead, the cricket and its designated plant were
22. removed from the experiment. Upon removal, we measured the height of the tallest blade of grass
23. and recorded the length of time the plant/cricket spent in the chamber. We also cut and weighed
24. above ground biomass to determine wet and dry mass. On day 28, we removed all remaining plants
25. from the experiment and recorded the final height of the tallest blade of grass. We calculated the
26. average daily growth rate in week four (day 21 to day 28) to control for plants that were removed
27. prematurely due to cricket death.

## 2.3 Gas Exchange Measurements

1. To assess light treatment effects on bluegrass physiology independent of herbivory, we
2. measured leaf photosynthetic responses on day 19 before crickets were placed into pots. We
3. measured leaf gas exchange in each light treatment using a LI-6400XT infrared gas analyzer with a
4. leaf chamber fluorometer attached (Li-Cor Biosciences; Lincoln, NE) following previously published
5. methods with slight modifications (Lemoine et al., 2018). Plants were removed from the growth
6. chamber temporarily for gas exchange measurements. The environmental conditions inside the leaf
7. chamber were standardized across measurements; leaf temperature was maintained at 20°C, relative
8. humidity was maintained between 40-50%, sample chamber flow rate was set to 200 μmol s-1, and
9. reference chamber CO2 concentration was set to 400 ppm. Low flow settings are commonly used for
10. small leaved grasses with low photosynthetic rates (Taylor, 2014). Leaf level gas exchange was
11. measured under two light conditions: dark and low light (10 μmol m2 s-1 (740 lx) photosynthetically
12. active radiation; PAR). Gas exchange in the dark provides an estimation of leaf respiration. The low
13. light level was the minimum amount of light provided by the Li-6400 light source; thus, we were
14. unable to measure photosynthesis under the tested ALAN conditions imposed here (<10 umols, <740
15. lux), but instead measured whether treatments had an impact on plant photosynthetic responses to
16. low levels of light. Results are reported in regard to light treatment in the growth chamber (urban
17. light or starlight). A newly emerged and fully expanded leaf from each individual (n= 10 individuals
18. per treatment) was inserted into the leaf chamber. Prior to measurements, leaves were dark adapted
19. for 2 hours under a dark box that allowed no light to enter. Leaves were left in the chamber for 2-5
20. minutes to equilibrate to chamber conditions before gas exchange parameters (photosynthesis or
21. respiration, and stomatal conductance) were recorded (average of three logged values taken in rapid
22. succession). Steady-state fluorescence (Fs) was measured continuously before exposing plants to a
23. saturating pulse of light (2750 μmol m−2 s−1 of blue light or ~203,500 lux (Thimijan and Heins, 1983)
24. to measure maximum chlorophyll fluorescence. Light inside the chamber was then switched to the
25. low light level (10 μmol m2 s-1). Once gas exchange reached stability, net photosynthetic rate, and
26. stomatal conductance were recorded, and a saturating pulse was applied to estimate photosystem II
27. efficiency (ΦPSII): ΦPSII = (Fm′ − Fs)/Fm’ where Fm’ represents chlorophyll fluorescence under
28. low light. As grass blades rarely fill the entire chamber, the measured leaf area was estimated using
29. width and length, and photosynthetic parameters, which are based on the area of the chamber (6 cm2),
30. were adjusted accordingly.

## 2.4 Data Analysis

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

# 3 Results

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

# 4 Discussion

1. Our study explored how low levels of artificial light at night, which are widespread across
2. ecosystems, may affect plants and plant-insect interactions. Contrary to our predictions, grass grown
3. under urban light conditions after 19 days did not have higher net photosynthetic rates than those
4. grown under starlight, nor did stomatal conductance, dark respiration, or ΦPSII differ significantly
5. between light treatments. However, plants under urban light conditions grew taller than plants grown
6. under starlight conditions during the initial 21 days of growth before crickets were introduced.
7. Additionally, we found no evidence that crickets under urban light consumed more plant matter than
8. crickets in starlight treatments, and survival rates of crickets did not differ between treatments. The
9. results from this study suggest that low levels of ALAN may not have significant effects on grass
10. photobiology but may affect plant height.
11. Studies investigating grass responses to higher levels of illumination (e.g., 4±1 μ㏖?m-2?s-1
12. or 296 lux) found that plant photoreceptors were damaged causing changes to flowering phenology
13. (Thimijan and Heins, 1983; Shin et al., 2010; Bennie et al., 2016). The lower levels of light tested
14. here were likely not bright enough to induce these changes in bluegrass. Plants often use nighttime
15. darkness to repair damage from UV rays, suggesting the low levels of ALAN in our treatments may
16. be dark enough for plants to continue to repair damaged cells and photoreceptors (Singhal et al.,
17. 2018). Moreover, net photosynthesis is a dynamic measurement that can vary within samples due to
18. time and day(Miller et al., 1996) and our single measurement at the end of week 3 may not have
19. captured treatment differences occurring at other times.
20. We found no difference in stomatal conductance or respiration between plants grown in urban
21. light and starlight. Other studies have noted differences in stomatal density and stomatal opening and
22. closing in the presence of ALAN (Takemiya et al., 2005; Shimazaki et al., 2007). Another study
23. found that yellow-poplar trees exposed to ALAN (high pressure sodium lighting ranging from 82 lx
24. to 4100 lx) for three years resulted in reduced nighttime stomatal conductance (Kwak et al., 2018). It
25. is possible that our light levels were too low, or grass was not subjected to our light levels for a long
26. enough duration to induce such responses. Reduced chlorophyll and rubisco concentration has been
27. observed in phytoplankton grown under low light levels (6.6 lux;(Poulin et al., 2014), and light as
28. low as 3.5 lux has induced flowering in tree species across the United Kingdom (Ffrench-Constant et
29. al., 2016). We also observed no treatment effects on photosystem II efficiency despite other studies
30. noting adverse reactions in these physiological responses to light pollution (Zhang and Reisner, 2019;
31. Meravi and Prajapati, 2020). Kentucky Bluegrass might be more adaptable to changing light regimes
32. given that it is commonly used as a turf grass selected for its resilience to drought and heat stress
33. (Wang and Huang, 2004). We observed a faster growth rate for grasses grown under urban light
34. conditions compared to starlight conditions. Plant growth rate is determined by a variety of factors,
35. including, but not limited to, photosynthetic rate, specific leaf area, leaf mass fraction, and nitrogen
36. absorption rate(Poorter et al., 1991; Osone et al., 2008). Although we found no difference in net
37. photosynthetic rate between treatments, growth rate differences could have been due to greater
38. allocation to leaf area in urban light(Poorter and Remkes, 1990), although we did not measure such
39. attributes.
40. ALAN is known to alter photoperiod detection in multiple organisms (Bennie et al., 2016)
41. and these changes in photoperiod can impact plant growth and flowering (Cathey and Campbell,
42. 1975; Blanchard and Runkle, 2010; Basler and Körner, 2012; Craig and Runkle, 2016). Increased
43. growth and biomass have been noted in *Poaceae* species when exposed to high levels of ALAN
44. ranging from 0.349 - 1.145μmols m² sec⁻¹ from metal halide bulbs (Flowers and Gibson, 2018),
45. which is approximately 24.78 - 81.30 lux (Thimijan and Heins, 1983). Since we noted no change in
46. Kentucky Bluegrass, photoperiod detection may not have been disrupted at our lower levels of
47. ALAN, or it may have caused undetectable or non-measured physiological responses.
48. While animals rely on plants as a food source and shelter, we found no evidence that low-
49. level light pollution would impact these typical interactions between plants and insects. Artificial
50. light at the level of 0.3 lux was not significant enough to mask natural light cues in herbivores, nor
51. mislead herbivores in foraging behaviors, but light pollution at higher levels could modify these
52. interactions(Gaston et al., 2013; Macgregor et al., 2015; Bennie et al., 2016; Knop et al., 2017). High
53. levels of ALAN could mask lunar cues, disrupting invertebrate behavior and feeding patterns and
54. could attract invertebrates to artificially lit structures, deterring them from normal behavioral patterns
55. (Longcore and Rich, 2004; Seymoure, 2018; Dominoni et al., 2020; Sanders et al., 2021).
56. Overall, our research detected few changes to plant physiology at low levels of urban light,
57. suggesting that low levels of ALAN may not be as harmful to community interactions as predicted.
58. Other studies conducted at high levels of ALAN suggest artificial light can induce large changes in
59. physiology and community interactions(Longcore and Rich, 2004; Gaston et al., 2013; Seymoure et
60. al., 2019a). There may be a threshold level at which artificial light becomes harmful, causing
61. detrimental effects to individual and ecosystem function with additional increases in intensity and
62. duration. Understanding and identifying this threshold would allow for more effective management
63. of night skies and natural light conditions(Dominoni et al., 2020). With estimates suggesting two
64. thirds of Key Biodiversity Areas experience ALAN(Seymoure et al., 2019a; Garrett et al., 2020), it is
65. important to identify the level at which artificial light becomes harmful and how natural night skies
66. can be managed.

# 5 Acknowledgements

1. This work was supported through a Zoological Lighting Institute Grants-In-Aid of Research
2. grant awarded to MC and CB. MC was awarded a SEEDS grant to present this research at the 2019
3. meeting of the Ecological Society of America (ESA) where we received excellent feedback from the
4. ESA community. Furthermore, this work was supported through the Colorado State University
5. Honors Program. We are grateful for support from the Smith Lab, the Sound and Light Ecology
6. Team at Colorado State University, and the Natural Sounds and Night Skies Division of the Natural
7. Park Service. Jeremy White, Tammy Brenner, and Bob Meadows were foundational to the success of
8. this study.
9. *The authors declare that the research was conducted in the absence of any commercial or financial*
10. *relationships that could be construed as a potential conflict of interest*.
11. 278

# 6 References

1. Alaasam, V. J., Duncan, R., Casagrande, S., Davies, S., Sidher, A., Seymoure, B., et al. (2018). Light
2. at night disrupts nocturnal rest and elevates glucocorticoids at cool color temperatures. *J Exp*
3. *Zool A Ecol Integr Physiol*. doi:10.1002/jez.2168.
4. Aubé, M. (2015). Physical behaviour of anthropogenic light propagation into the nocturnal
5. environment. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 370. doi:10.1098/rstb.2014.0117.
6. Basler, D., and Körner, C. (2012). Photoperiod sensitivity of bud burst in 14 temperate forest tree
7. species. *Agric. For. Meteorol.* 165, 73–81.
8. Bennie, J., Davies, T. W., Cruse, D., and Gaston, K. J. (2016). Ecological effects of artificial light at
9. night on wild plants. *J. Ecol.* 104, 611–620.
10. Biberman, L. M., Dunkelman, L., Fickett, M. L., and Finke, R. G. (1966). Levels of Nocturnal
11. Illumination. Institute for Defense Analyses, Research and Engineering Support Division
12. Available at: https://apps.dtic.mil/sti/citations/AD0632918 [Accessed March 26, 2021].
13. Blanchard, M. G., and Runkle, E. S. (2010). Intermittent light from a rotating high-pressure sodium
14. lamp promotes flowering of long-day plants. *HortScience* 45, 236–241.
15. Briggs, W. R., and Christie, J. M. (2002). Phototropins 1 and 2: versatile plant blue-light receptors.
16. *Trends Plant Sci.* 7, 204–210.
17. Buxton, R. T., Seymoure, B. M., White, J., Angeloni, L. M., Crooks, K. R., Fristrup, K., et al. (2020).
18. The relationship between anthropogenic light and noise in U.S. national parks. *Landsc. Ecol.* 35, 298 1371–1384.
19. Cathey, H. M., and Campbell, L. E. (1975). Security lighting and its impact on the landscape.
20. *Journal of arboriculture*. Available at: https://agris.fao.org/agris-
21. search/search.do?recordID=US201303079623.
22. Celaya, R. B., and Liscum, E. (2005). Phototropins and Associated Signaling: Providing the Power of
23. Movement in Higher Plants\P. *Photochem. Photobiol.* 81, 73–80.
24. Craig, D. S., and Runkle, E. S. (2016). An intermediate phytochrome photoequilibria from night-
25. interruption lighting optimally promotes flowering of several long-day plants. *Environ. Exp.*

306 *Bot.* 121, 132–138.

1. Davies, T. W., Bennie, J., Inger, R., and Gaston, K. J. (2013). Artificial light alters natural regimes of
2. night-time sky brightness. *Sci. Rep.* 3, 1722.
3. Dietrich, P., Sanders, D., and Hedrich, R. (2001). The role of ion channels in light‐dependent
4. stomatal opening. *J. Exp. Bot.* 52, 1959–1967.
5. Dominoni, D. M., Carmona-Wagner, E. O., Hofmann, M., Kranstauber, B., and Partecke, J. (2014).
6. Individual-based measurements of light intensity provide new insights into the effects of
7. artificial light at night on daily rhythms of urban-dwelling songbirds. *J. Anim. Ecol.* 83, 681– 314 692.
8. Dominoni, D. M., Halfwerk, W., Baird, E., Buxton, R. T., Fernández-Juricic, E., Fristrup, K. M., et
9. al. (2020). Why conservation biology can benefit from sensory ecology. *Nat Ecol Evol* 4, 502– 317 511.
10. Dominoni, D., Quetting, M., and Partecke, J. (2013). Artificial light at night advances avian
11. reproductive physiology. *Proc. Biol. Sci.* 280, 20123017.
12. Ffrench-Constant, R. H., Somers-Yeates, R., Bennie, J., Economou, T., Hodgson, D., Spalding, A., et
13. al. (2016). Light pollution is associated with earlier tree budburst across the United Kingdom. 322 *Proc. Biol. Sci.* 283. doi:10.1098/rspb.2016.0813.
14. Flowers, N. D., and Gibson, D. J. (2018). Quantified effects of artificial versus natural nighttime
15. lighting on the Eurasian grasses: Bothriochloa bladhii (Poaceae) and Bothriochloa ischaemum
16. (Poaceae) and the North American grasses: Panicum virgatum (Poaceae) and Sorghastrum
17. nutans (Poaceae). *J. Torrey Bot. Soc.* 145, 147–155.
18. Garrett, J. K., Donald, P. F., and Gaston, K. J. (2020). Skyglow extends into the world’s Key
19. Biodiversity Areas. *Anim. Conserv.* 23, 153–159.
20. Gaston, K. J., Bennie, J., Davies, T. W., and Hopkins, J. (2013). The ecological impacts of nighttime
21. light pollution: a mechanistic appraisal. *Biol. Rev. Camb. Philos. Soc.* 88, 912–927.
22. Gaston, K. J., Davies, T. W., Nedelec, S. L., and Holt, L. A. (2017). Impacts of Artificial Light at
23. Night on Biological Timings. *Annu. Rev. Ecol. Evol. Syst.* 48, 49–68.
24. Gaston, K. J., Duffy, J. P., and Bennie, J. (2015). Quantifying the erosion of natural darkness in the
25. global protected area system. *Conserv. Biol.* 29, 1132–1141.
26. Hammond, W. A. (1935). Use and regeneration of Drierite. *J. Chem. Educ.* 12, 445.
27. Jones, B. M., Seymoure, B. M., Comi, T. J., and Loew, E. R. (2020). Species and sex differences in
28. eye morphometry and visual responsivity of two crepuscular sweat bee species (Megalopta spp.,
29. Hymenoptera: Halictidae). *Biol. J. Linn. Soc. Lond.* 130, 533–544.
30. Knop, E., Zoller, L., Ryser, R., Gerpe, C., Hörler, M., and Fontaine, C. (2017). Artificial light at
31. night as a new threat to pollination. *Nature* 548, 206–209.
32. Kwak, M. J., Je, S. M., Cheng, H. C., Seo, S. M., Park, J. H., Baek, S. G., et al. (2018). Night Light-
33. Adaptation Strategies for Photosynthetic Apparatus in Yellow-Poplar (Liriodendron tulipifera
34. L.) Exposed to Artificial Night Lighting. *For. Trees Livelihoods* 9, 74.
35. Kyba, C. C. M., Kuester, T., Sánchez de Miguel, A., Baugh, K., Jechow, A., Hölker, F., et al. (2017).
36. Artificially lit surface of Earth at night increasing in radiance and extent. *Sci Adv* 3, e1701528.
37. Kyba, C. C. M., Tong, K. P., Bennie, J., Birriel, I., Birriel, J. J., Cool, A., et al. (2015). Worldwide
38. variations in artificial skyglow. *Sci. Rep.* 5, 8409.
39. Lemoine, N. P., Griffin-Nolan, R. J., Lock, A. D., and Knapp, A. K. (2018). Drought timing, not
40. previous drought exposure, determines sensitivity of two shortgrass species to water stress. 350 *Oecologia* 188, 965–975.
41. Longcore, T., and Rich, C. (2004). Ecological light pollution. *Front. Ecol. Environ.* 2, 191–198.
42. Luginbuhl, C. B., Duriscoe, D. M., Moore, C. W., Richman, A., Wesley Lockwood, G., and Davis,
43. D. R. (2009). From the Ground Up II: Sky Glow and Near-Ground Artificial Light Propagation
44. in Flagstaff, Arizona. *PASP* 121, 204.
45. Macgregor, C. J., Pocock, M. J. O., Fox, R., and Evans, D. M. (2015). Pollination by nocturnal
46. Lepidoptera, and the effects of light pollution: a review. *Ecol. Entomol.* 40, 187–198.
47. McNaughton, S. J. (1983). Compensatory Plant Growth as a Response to Herbivory. *Oikos* 40, 329– 358 336.
48. Meravi, N., and Prajapati, S. K. (2020). Effect street light pollution on the photosynthetic efficiency
49. of different plants. *Biological Rhythm Research* 51, 67–75. 361 doi:10.1080/09291016.2018.1518206.
50. Miller, D. P., Howell, G. S., and Flore, J. A. (1996). A Whole-plant, Open, Gas-exchange System for
51. Measuring Net Photosynthesis of Potted Woody Plants. *HortScience* 31, 944–946. 364 doi:10.21273/hortsci.31.6.944.
52. Osone, Y., Ishida, A., and Tateno, M. (2008). Correlation between relative growth rate and specific
53. leaf area requires associations of specific leaf area with nitrogen absorption rate of roots. *New*

367 *Phytol.* 179, 417–427.

1. Owens, A. C. S., Cochard, P., Durrant, J., Farnworth, B., Perkin, E. K., and Seymoure, B. (2020).
2. Light pollution is a driver of insect declines. *Biological Conservation* 241, 108259. 370 doi:10.1016/j.biocon.2019.108259.
3. Owens, A. C. S., and Lewis, S. M. (2018). The impact of artificial light at night on nocturnal insects:
4. A review and synthesis. *Ecol. Evol.* 8, 11337–11358.
5. Polis, G. A., Power, M. E., and Huxel, G. R. (2004). *Food Webs at the Landscape Level*. University
6. of Chicago Press.
7. Poorter, H., and Remkes, C. (1990). Leaf area ratio and net assimilation rate of 24 wild species
8. differing in relative growth rate. *Oecologia* 83, 553–559.
9. Poorter, H., van der Werf, A., Atkin, O. K., and Lambers, H. (1991). Respiratory energy
10. requirements of roots vary with the potential growth rate of a plant species. *Physiologia*

379 *Plantarum* 83, 469–475. doi:10.1034/j.1399-3054.1991.830321.x.

1. Poulin, C., Bruyant, F., and Laprise, M. H. (2014). The impact of light pollution on diel changes in
2. the photophysiology of Microcystis aeruginosa. *J. Plankton Res.* Available at:
3. https://academic.oup.com/plankt/article-abstract/36/1/286/1524459.
4. R Development Core Team (1999). *The R Reference Manual: Base Package*. Network Theory.
5. Read, J. C., Reinert, J. A., Colbaugh, P. F., and Knoop, W. E. (1999). Registration of
6. “Reveille”hybrid bluegrass. *Crop Sci.* 39, 590–590.
7. Sanders, D., Frago, E., Kehoe, R., Patterson, C., and Gaston, K. J. (2021). A meta-analysis of
8. biological impacts of artificial light at night. *Nat Ecol Evol* 5, 74–81.
9. Sanders, D., and Gaston, K. J. (2018). How ecological communities respond to artificial light at
10. night. *J Exp Zool A Ecol Integr Physiol* 329, 394–400.
11. Seymoure, B., Buxton, R., White, J., Linares, C., Fristrup, K., Crooks, K., et al. (2019a).
12. Anthropogenic Light Disrupts Natural Light Cycles in Critical Conservation Areas. 392 doi:10.2139/ssrn.3439670.
13. Seymoure, B. M. (2018). Enlightening Butterfly Conservation Efforts: The Importance of Natural
14. Lighting for Butterfly Behavioral Ecology and Conservation. *Insects* 9. 395 doi:10.3390/insects9010022.
15. Seymoure, B. M., Linares, C., and White, J. (2019b). Connecting spectral radiometry of
16. anthropogenic light sources to the visual ecology of organisms. *J. Zool.* 308, 93–110.
17. Shimazaki, K.-I., Doi, M., Assmann, S. M., and Kinoshita, T. (2007). Light regulation of stomatal
18. movement. *Annu. Rev. Plant Biol.* 58, 219–247.
19. Shin, J. H., Jung, H. H., and Kim, K. S. (2010). Night Interruption Using Light Emitting Diodes
20. (LEDs) Promotes Flowering of Cyclamen persicum in Winter Cultivation. *Horticulture*
21. *Environment and Biotechnology* 51, 391–395.
22. Singhal, R. K., Kumar, M., and Bose, B. (2018). Ecophysiological Responses of Artificial Night
23. Light Pollution in Plants. *Russ. J. Plant Physiol.*, 1–13.
24. Spitschan, M., Aguirre, G. K., Brainard, D. H., and Sweeney, A. M. (2016). Variation of outdoor
25. illumination as a function of solar elevation and light pollution. *Sci. Rep.* 6, 26756.
26. Suplick-Ploense, M. R., and Qian, Y. (2005). Evapotranspiration, rooting characteristics, and
27. dehydration avoidance: Comparisons between hybrid bluegrass and Kentucky bluegrass. *Int.*
28. *Turfgrass Soc. Res. J* 10, 891–898.
29. Takemiya, A., Inoue, S.-I., Doi, M., Kinoshita, T., and Shimazaki, K.-I. (2005). Phototropins
30. Promote Plant Growth in Response to Blue Light in Low Light Environments. *Plant Cell* 17, 412 1120–1127.

413 Taylor, J. R. (2014). A Simple Inquiry-Based Lab for Teaching Osmosis. *Am. Biol. Teach.* 76, 265– 414 269.

1. Therneau, T., and Lumley, T. (2009). survival: Survival analysis, including penalised likelihood. *R*
2. *package version* 2.
3. Thimijan, R. W., and Heins, R. D. (1983). Photometric, radiometric, and quantum light units of
4. measure: a review of procedures for interconversion. *HortScience* 18, 818–822.
5. Wada, M., Kagawa, T., and Sato, Y. (2003). Chloroplast movement. *Annu. Rev. Plant Biol.* 54, 455– 420 468.
6. Wang, Z., and Huang, B. (2004). Physiological recovery of Kentucky bluegrass from simultaneous
7. drought and heat stress. *Crop Sci.* 44, 1729–1736.
8. Weissman, D. B., Rentz, D. C. F., and Others (1977). Feral house crickets Acheta domesticus
9. (L.)(Orthoptera: Gryllidae) in southern Calif. *Entomol. News* 88, 246–248.
10. Zhang, J. Z., and Reisner, E. (2019). Advancing photosystem II photoelectrochemistry for semi-
11. artificial photosynthesis. *Nature Reviews Chemistry* 4, 6–21. 427

428

429

430

431

432

433

434

435

436

437

438

439 **Table 1** MANOVA table of the gas exchange results evaluating differences in photosynthesis,

440 stomatal conductance in dark, stomatal conductance in light, fluorescence, and photosystem II

441 efficiency.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  |  | ***df*** | **Pillai** | ***f*** | ***p*** |
|  | **Treatment** | **1** | **0.18** | **0.45** | **0.83** |
|  | **Block** | **3** | **0.95** | **1.09** | **0.40** |
|  | **Residuals** | **17** |  |  |  |
| 442 |  |  |  |  |  |

443 **Table 2** ANOVA table comparing mean grass height at day 21 across light treatments and blocks. \*

444 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** |  |  |
| 445 |  |  |  |  |  |  |

446 **Table 3** ANOVA table showing the effects of light treatment, cricket treatment, and block (plus

447 interactions between light and cricket treatment and cricket and block treatment) on daily percent

448 change in grass height between day 21 and the end of the experiment. \* indicates a significant

449 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 x 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** |  |  |
| 450 |  |  |  |  |  |  |
| 451 |  |  |  |  |  |  |
| 452 |  |  |  |  |  |  |

1. **Figure 1:** Aerial view of treatment groups in the growth chamber after crickets were introduced (day
2. 21-28). The treatment groups were arranged in a block test pattern with 4 blocks of urban light
3. treatments and 4 blocks of starlight treatments, totaling 8 groups (A-H). Within each block (A-H),
4. nine plants (every other one) had a cricket.
5. **Figure 2: (A)** Net photosynthesis across light treatments, measured under low light conditions (10
6. μmols m-2 s-1 of light) and **(B)** stomatal conductance across light treatments. **(C)** Photosystem II
7. efficiency is measured using a saturating pulse (ΦPSII): ΦPSII = (Fm′ − Fs)/Fm’ where Fm is
8. chlorophyll fluorescence under low light. **(D)** Dark respiration measured under low light level (<10
9. μmols m-2 s-1 of light). There were no differences in net photosynthesis, stomatal conductance,
10. Photosystem II efficiency, or dark respiration between light treatments.
11. **Figure 3: (A)** Bluegrass height at day 21 separated by light treatment when no crickets were present.
12. Grass in urban light was taller than grass in starlight conditions. **(B)** Daily percent change in height of
13. grass (change from day 21 to day 28 divided by the number of days in the chamber) separated by
14. light treatment. There was no difference in daily percent change across light or cricket treatments.
15. **Figure 4:** Survival probability of crickets. **(A)** Survival probability of crickets under urban light and
16. starlight treatments. **(B)** Survival probability of crickets under urban light and starlight treatments,
17. split by sex in each treatment group. In all both comparisons **(A-B)**, there were no differences in
18. survival.