INVASION NOTE

Light pollution affects invasive and native plant traits important to plant competition and herbivorous insects

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Abstract Invasions in urban settings have been understudied in terms of how invasions are impacted by uniquely urban stressors, such as streetlights. Plant physiology and phenology are impacted by artificial light at night (ALAN), but no studies have yet examined if light pollution differentially affects native versus invasive plant species. We tested the hypothesis that ALAN affects plant traits important to plant fitness and susceptibility to herbivory and whether they differ between invasive versus native grass species. We found that aboveground production of invasive cheatgrass was $>5 \times$ greater under ALAN than any other species in any treatment, and ALAN also altered plant traits important to herbivory. This suggests that ALAN may influence the outcomes of interspecific interactions. As urbanization increases, its role in invasion biology becomes more important, especially when an urban disturbance such as ALAN benefits the growth of invasive species.

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Introduction

Urban settings present plants with many disturbances, including synthetic pollutants, extreme trampling by foot or wheeled vehicles, and artificial light. However, within ecological research, there has been a particular "blind spot" with regard to invasions in urban settings (Cavin and Kull 2017), including exploring the impacts of the uniquely urban stressor of streetlights. Artificial light at night (ALAN) is an important disturbance potentially capable of shaping plant communities within urban habitats (e.g. Speißer et al. 2020). Plant physiology and phenology can be impacted by ALAN (e.g. Bennie et al. 2016; Grenis and Murphy 2019; Massetti 2018; Xu et al. 2019), but no studies have examined if ALAN differentially affects native versus invasive plant species. Invasive plants species often thrive under disturbance (Lozon and MacIsaac 1997), thus the extended photoperiod from a disturbance such as ALAN may provide a competitive advantage that could threaten native plant communities. Here we test the hypothesis that ALAN affects plant traits important to plant fitness and susceptibility to herbivory (above and belowground

biomass, leaf toughness, and nutrient content as measured by C:N ratio). We also test whether the effect of ALAN on these plant traits differs between exotic, invasive grasses and native grass species, which has not been previously investigated. If ALAN promotes the growth of invasive plants, then native plant conservation strategies would benefit greatly from additional research on the impact of ALAN on growth and survival.

Materials and methods

Study system

We studied 6 grass species commonly found in shortgrass prairie fragments throughout the Denver-metro area. These fragments frequently contain invasive species of forbs and grasses and are exposed to ALAN from surrounding urban areas. We used 4 common, urban grass species native to shortgrass prairies: alkali sacaton (*Sporobolus airoides* Torr.), buffalo grass (*Buchloe dactyloides* Nutt.), blue grama (*Bouteloua gracilis* [H.B.K.] Lag.), and western wheatgrass (*Agropyron smithii* Rydb.). We also used 2 common invasive species introduced for livestock grazing and erosion prevention: cheatgrass (*Bromus tectorum* L.) and smooth brome (*Bromus inermis* Leyss.)

Plant performance

To investigate the effects of ALAN, we initiated a greenhouse experiment to test the effects of nocturnal artificial lighting on aboveground and belowground biomass, leaf toughness, and nutrient content (C:N ratio) of the grasses described above. For each of the 6 grass species, we placed 10 seeds in each of 60 515cm^3 cone-tainers (i.e., 360 cone-tainers, hereafter "pots") filled with garden soil. We evenly and randomly distributed the 6 species into flats (1 flat= 24 pots). We placed half the flats (180 pots) into a partitioned greenhouse lit overhead by high-pressure sodium lamps (used as streetlights in many cities) timed to illuminate from 21:00 to 06:00, mirroring summer streetlight illumination. We placed the other half of the flats in an area of the greenhouse with the same temperature and humidity settings (the two areas are open to each other) but with only ambient natural light

as a control (methods for plant care are in the Supplementary Information).

We began harvests after each species had sufficient biomass in each pot for all plant measurements (smooth brome at week 10, blue grama at week 11, cheatgrass and western wheatgrass at week 25; these start dates for harvest varied due to each species' germination time). Every 3 weeks, we randomly selected 5 pots from each species and light treatment to harvest, resulting in 6 harvests over a total of 18 weeks for blue grama, cheatgrass, smooth brome, and western wheat (n=5 replicate pots harvested each date). Alkali sacaton and buffalo grass had low germination and growth, so were only harvested at the end of the experiment (week 43). We measured the toughness of each individual plant in each pot. For each plant we measured the toughness of the first green blade of grass per culm using the "cup-string method" (Feeny 1970). After we measured leaf toughness, we washed the roots and shoots and then placed all harvested material from a given pot in individual paper bags in a drying oven (60 °C, 3 days) to measure dry tissue biomass. To measure C:N ratio, we ground the aboveground biomass in a mixer mill (Retsch MM400) and sent processed samples to the Cornell Stable Isotope Laboratory for nutrient analysis to be analyzed for %N and %C using an elemental analyzer-stable isotope ratio mass spectrometer system.

Statistical analyses

We used a 2-way ANOVA with *light treatment*, *species*, and *light treatment x species* interaction as the independent variables; aboveground biomass, aboveground:belowground ratio, C:N ratio, and toughness were our dependent variables. When needed, we used a log transformation to meet assumptions of normality and variance. To determine whether plant traits were differentially affected by ALAN over time, we repeated the analysis for the samples taken at different harvest periods. We used RStudio 1.1.453 for all analyses.

Results

ALAN improved aboveground biomass growth only for cheatgrass (p=0.005), an invasive species (*treatment x species*: $F_{5,98} = 2.89$, $p = 0.02$; Fig. 1a). Indeed,

cheatgrass under ALAN had >5 times the aboveground biomass than any other grass species, regardless of light treatment (Fig. 1a). However, when comparing the aboveground:belowground ratio, ALAN affected only the native buffalo grass ($p=0.01$), which invested more energy into aboveground biomass than belowground biomass when exposed to ALAN (Fig. 1b). ALAN did not influence plant toughness for any species (*treatment x species* : $F_{5,104} = 0.69$, $p = 0.63$; Fig. 1c). Lastly, ALAN increased the C:N ratio for the native buffalo grass ($p=0.02$) and the exotic cheatgrass ($p=0.002$) (*treatment x species*: $F_{5,118} = 2.55$, $p = 0.03$ Fig. 1d). Some of our sample sizes for the analyses conducted after the final harvest were rather small either because few of the plants of some species survived or because for four plant species (blue grama, western wheatgrass, cheatgrass, smooth brome) we only compared plants harvested at the end of the experiment in this analysis. To determine if we had a sufficient sample size for our non-significant results, we used post hoc power

analyses to test for the probability of type-II error with our non-significant results (Supplementary Information). We also found that ALAN affected some plant traits differently over time (Supplementary Information and Figures S1–S4).

Discussion

Our study demonstrates that ALAN may be a disturbance that favors the growth of some invasive plant species and also affects traits that are important to herbivores. These results suggest that under streetlights, invasive species such as cheatgrass may be able to use resources more quickly or efficiently to outcompete native species, thereby directly affecting invasion dynamics in urban environments (see also Murphy et al. 2021). Notably the C:N ratio for cheatgrass was also significantly greater when grown under ALAN with plants having a C:N ratio that was
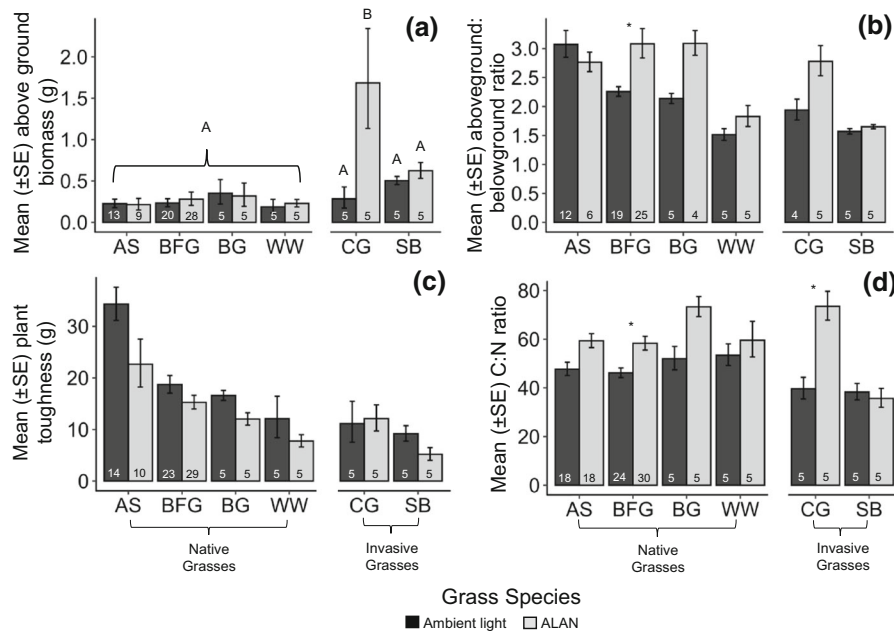
Fig. 1 Effects of ALAN on **a** aboveground dry biomass by seedling, **b** aboveground:belowground ratio, **c** plant toughness by seedling, and **d** C:N ratio of grass species grown in the greenhouse experiment. Dark gray bars indicate the control treatment (ambient) and light gray bars indicate the ALAN treatment (streetlights). Native species: AS = alkali sacaton, BFG = buffalo grass, BG = blue grama, WW = western wheatgrass. Invasive species: CG = cheatgrass, SB = smooth brome. Bars show the mean of each measure ± SE of root transformed data in A and C and log transformed data in B and D; numbers in bars indicate sample size for the sixth and last harvest for BG, WW, CG and SB (for other harvest data see supplementary information) and only harvest for AS and BFG. Letters in (**a**) indicate significant differences between treatments and plant species and asterisks in (**b**–**d**) indicate significant differences between treatments ($p < 0.05$)

$\sim 2 \times$ larger than when grown in ambient conditions. Nitrogen is a limiting nutrient for herbivores and thus plants with high C:N ratios are less nutritious for herbivores. Thus, our results show that ALAN affects traits important for plant-plant competition but also trophic interactions.

The mechanisms by which ALAN affects plant physiology remain unclear. Certain plants exposed to longer photoperiods have different photosynthetic capabilities and changes in cellular processes important to photosynthesis (Briggs 2006); alterations to photosynthetic pathways may reduce the amount of energy available for secondary metabolism (plant defense traits) or nutrient uptake. Regardless of the mechanism, changes to plant traits like toughness and C:N ratio are important as they affect host plant quality for invertebrate herbivores (Price et al. 2011), which can have cascading effects throughout a community (Murphy et al. 2012). Plants grown under ALAN may create a trade-off for invertebrate herbivores between consumption ability and nutrition.

Our study is the first to show that cheatgrass, a highly invasive grass species, responds more favorably to ALAN than native grasses. We found that ALAN alters plant traits important to competition and herbivory, suggesting mechanisms by which ALAN may influence interspecific interactions. Resource availability and acquisition can dramatically differ in urban environments compared to wild habitats, and ALAN could be an important contributing factor to how plant communities are structured in urban habitats. As urbanization increases, its role in understanding invasion biology becomes more important, especially when an urban disturbance such as ALAN benefits the growth of invasive species.

Declaration

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

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