Artificial light at night (ALAN) influences understory plant traits through ecological processes: a two-year experiment in a rubber plantation in China

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ABSTRACT

Artificial light at night (ALAN) demonstrated a new ecological factor that influences organisms through multi-approach. Yet, the impacts of ALAN on understory plants remain largely unknown. We evaluated whether ALAN would affect leaf mass per area (LMA) of understory plants through a two-year field light experiment in a tropical rubber plantation in south China. We hypothesized that ALAN could impact the understory in two ways: by directly supplementing light to aboveground plant parts (which increases LMA) and indirectly affecting soil nutrient composition by attracting insects (which decreases LMA). We selected two species: *Colocasia gigantea*, representing shade-torelant species, and *Melastoma candidum*, representing light-demanding species. We measured canopy openness, LMA, soil nutrients, and individual distance away from light resources. We found a negative relationship between LMA and the strength of ALAN, indicating that ALAN may influence LMA more indirectly by enhancing soil nutrient availability rather than directly acting as a light resource. This relationship was significant for *Colocasia gigantea* but not for *Melastoma candidum*. These results suggest that ALAN might have complex and species-specific impacts on the understory ecosystem.

KEY WORDS *Colocasia gigantea*, *Melastoma candidum*, artificial light at night, functional traits, leaf mass per area, specific leaf area, understory

INTRODUCTION

Artificial light at night (ALAN), a leading contributor to light pollution, has disrupted ecological processes since the early 20th century (Longcore and Rich 2004, Gaston et al. 2013, Bennie et al. 2016). A recent study estimated that around 23% of the world's inhabited land surfaces, accounting for over 80% of the global population, are subject to the adverse effects of light pollution (Falchi et al. 2016). Although the intensity of ALAN varies several orders of magnitude from faint skyglow reflected from distant cities to direct illumination of urban and suburban vegetation (Bennie et al. 2016), ALAN influences the behavior or physiology of broad ranges of taxonomic groups, including mammals, birds, reptiles, amphibians, fishes, invertebrates, and plants (Rich and Longcore 2006, Loss et al. 2014, Falcón et al. 2020, Forsburg et al. 2021). It could also alter ecosystem functions (Rich and Longcore 2006, Falcón et al. 2020). For example, ALAN attracts insects and interferes with their movement, foraging, reproduction, and development (Owens et al. 2020, Boyes et al. 2021, Yang and Nakamura 2022). These interferences have been linked to declines in insect populations (Boyes et al. 2021). Unlike animals, only a handful of studies have been published on the effects of ALAN on plants (Bennie et al. 2016, Speißer et al. 2021, Liu et al. 2022). Speißer et al. (2021) conducted plant growth experiments with and without weak ALAN (28 lux: within the range of light intensities at ground level under street lights) and showed that ALAN increases the biomass of herbaceous plants. Their results suggest that even weak ALAN acts as a light resource for plant growth. However, few studies have examined the effects of ALAN on plant functional traits in conditions close to their natural environment.

ALAN might, directly and indirectly, affect plant leaf functional traits. First, ALAN might directly affect plant leaf functional traits, such as leaf mass per area (LMA), because ALAN could work as an additional light resource. Although LMA is driven by inherent genetic mechanisms (Asner et al. 2011), environmental stresses (temperature, water, and light) also shape LMA. Plants can sense light through photoreceptors, allowing them to respond to four parameters of their light environment: light spectral quality, light intensity, light direction, and light duration (Rich and Longcore 2006, Paik and Huq 2019). Terashima et al. (2006) showed that the light-saturated rate of leaf photosynthesis per unit area is highly correlated with leaf structural parameters such as leaf thickness, leaf mass per area, mesophyll surface area, and chloroplast surface area, resulting in sun leaves being thicker than shade leaves as the height of the palisade tissue in sun leaves is greater than that in shade leaves. For individual species, LMA was proportional with species distributions along the insolation gradient and was significantly higher in evergreen versus deciduous species (Ackerly et al. 2002, Niinemets et al. 2004, Onoda et al. 2008). Moreover, among a local community, Ackerly et al. (2002) demonstrated that the average values of LMA significantly increased with increasing potential diurnal insolation (PDI).

On the other hand, ALAN might indirectly affect plant leaf functional traits because ALAN has the potential to increase soil fertility by attracting insects. Many insects orient themselves by maintaining a constant angle to light rays and are attracted by light (Baker and Sadovy 1978, Sotthibandhu and Baker 1979). Previous studies showed that 30–40% of insects die soon after approaching street lamps for collision, overheating, dehydration, or predation (Minnaar et al. 2015, Owens and Lewis 2018). Since nitrogen (N) and phosphorus (P) are the nutrients most frequently limiting primary productivity in forest ecosystems (Wright 2019), dead insects killed by ALAN could be important nutrient inputs for soil nutrients (Behie and Bidochka 2013). Soil resources, especially N and P availability, are known to affect LMA and leaf N and P contents (Wright et al. 2004, Katabuchi et al. 2012, de la Riva et al. 2016), and those effects are known to be opposite to the effects of light (Ackerly et al. 2002, Hernández-Vargas et al. 2019) (i.e., while strong light increases LMA but high levels of N availability decrease LMA).

In this study, we investigated the effects of ALAN on LMA of understory plants through a two-year experiment in a tropical rubber plant forest in south China. A previous study conducted under the same experimental setup at this site demonstrated that ALAN attracts ants (Yang and

Nakamura 2022). We selected two understory species as subjects of this experiment, each representing light-demanding and shade-torelant species, to discern differences in their responses to ALAN. Our hypothesis proposes that ALAN would influence the understory plants via two distinct pathways. The first would be a direct effect, with ALAN serving as a supplementary light resource for plants, increasing LMA. The second pathway would be an indirect effect, where ALAN enhances soil nutrient availability, decreasing LMA. To determine the relative importance of these two pathways, we estimated the influences of ALAN, daylight, and their interaction on LMA of the understory plants.

MATERIALS AND METHODS

Experimental setup

ALAN field experiments were located within the Xishuangbanna Tropical Botanical Garden (XTBG), China, in a rubber tree forest (N21°54’ E101°16’) where we set 5 plots and selected two plots for this experiment based on the natural distribution of the target plant species. In the study area, the average yearly temperature is recorded at 21.7 °C, accompanied by an average annual precipitation of 1557 mm. No fertilizer was used in the study area. LED lights (10W) were used to create an artificial light environment in all plots at night (Fig. 1). The LED system was programmed to function automatically from 8 pm to 5 am daily. A rechargeable lithium battery (12V/30Ah) and an electric timer controlled the timing and duration of the LED operation at night. The battery and LEDs were connected by electric wire and hung from a tree branch with a lampshade approximately 2 m from the ground. The light intensity of LED lights at the light sources was 372.8 ± 66.6 (mean ± SE) lux. The light intensity decreased with distance: 190.2 ± 26.5 lux at a radius of 1 m, 62.0 ± 4.9 lux at a radius of 2 m, and 9.9 ± 0.7 lux at a radius of 4 m. The light intensity was almost undetectable at 0 lux beyond 10 m. The experiment was set up in November 2019, and leaf disc samples were collected two years later, in November 2021.

Species Selection

We considered the understory conditions to select species, ensuring that at least 15 mature individuals were present from the light source to 10 m away from it. Essential criteria also included the species being part of functional groups, specifically evergreen species, and not belonging to nitrogen-fixing families such as Leguminosae. As a result, we chose two species, each from a different plot, for our study: *Colocasia gigantea*, representing shade-torelant species, and *Melastoma candidum* representing light-demanding species.

Measurements

We measured the horizontal distance and geographic orientation of each individual away from the LED using a tape measure representing the relative effects of ALAN. The canopy openness of each individual was on behalf of individual daylight interception, which was photographed by Nikon COOLPIX4500 with a fish-eye lens (Nikon FC-e8) and then measured using the R package *LeafArea* (Katabuchi 2015).

For leaf mass per area (LMA), we used a 1.0 cm diameter puncher instead of using whole-leaf LMA values, avoiding veins and leaf margins (Maenpuen et al. 2022). We chose five healthy leaves from each individual *M. candidum* plant, and between three to five healthy leaves from each individual *C. gigantea* plant. We then punched five leaf discs from each *M. candidum* leaf, and seven leaf discs from each leaf of *C. gigantea*.

For soil nutrients (N, C, P), we collected surface soil samples (0-10 cm depths) in five plots in June 2019 and June 2022 to investigate the general trends in soil nutrients. Detailed analysis of soil nutrients was conducted in the two selected plots. We took three replicates at the place under ALAN and 10 m away from ALAN separately from each plot. After sampling, the soils were air-dried at room temperature for one week, then sieved through 0.85-mm and 0.15-mm mesh finally used for total N, C measurements by combustion using an elemental analyzer (Vario MAX CN, Elementar Analysensysteme GmbH, Germany) and total P measurement by inductively coupled plasma atomic-emission spectrometer (iCAP7400, Thermo Fisher Scientific, USA). We then calculated the relative percentage change of each nutrient between the value in 2019 and 2022 to compare the soil nutrient change with ALAN's effect (sampled under ALAN) and without ALAN's effect (sampled 10 m away from ALAN).

Data Analysis

To analyze the effects of ALAN, daylight and their interaction on *M. candidum* and *C. gigantea*, we fitted a Bayesian linear mixed-effects model for each species. The leaf mass per area (LMA) of each leaf of each individual was modelled as a function of the distance from the ALAN source for each individual, the canopy openness of each individual, and the interaction between the distance from the ALAN source and the canopy openness. We transformed the distance from the ALAN source for each individual using a log and reciprocal function, as the intensity of ALAN diminish non-linearly with distance. Hereafter, we refer to the distance from the ALAN source for each individual as the ALAN effect and the canopy openness of each individual as the daylight effect. To account for non-independence among individuals of the same species, we included individuals as a random intercept in our models.

Posterior distributions of all parameters were estimated using the Hamiltonian Monte Carlo algorithm (HMC) implemented in Stan (Carpenter et al. 2017) using the weakly-informative priors

(Gelman et al. 2008). Convergence of the posterior distribution was assessed with the Gelman-Rubin statistic with a convergence threshold of 1.1 (Gelman et al. 2013) and effective sample sizes > 400 (Vehtari et al. 2021) for all parameters. All statistical analyses were conducted in R version 4.2.0 (R Core Team 2022) using the R package *targets* version 1.2.0 for workflow management (Landau et al. 2023). Codes are available at https://github.com/congz007/light_project.

RESULTS

The influence of artificial light at night (ALAN) and daylight on LMA had significant effects on the species *Colocasia gigantea* , while for *Melastoma candidum*, these effects were not significant (Fig. 2). In the case of *C. gigantea*, ALAN led to a decrease in the average individual leaf mass per area (LMA) value (Table 1, slope: -0.1052 [95% CI: -0.1500, -0.0613]). Although *M. candidum* showed a similar decrease in LMA value in response to ALAN (Table 1, slope: -0.0434 [95% CI: -0.1147, 0.0278]), this change was not statistically significant. The interaction of the effects of ALAN and daylight did not yield any significant results for both species (Table 1).

Soil nutrients decreased from 2019 to 2022 [$X_{2022}/X_{2019} < 1$, where X represents carbon (C), nitrogen (N), and phosphorus (P)] across all of the locations, regardless of the distance away from ALAN. However, the relative percentage change in each soil nutrient demonstrated that the locations under ALAN sustained more nutrients in 2022 ($C_{2022}/C_{2019} = 0.919$, $N_{2022}/N_{2019} = 0.948$, $P_{2022}/P_{2019} = 0.537$) compared to the locations 10 m away from ALAN ($C_{2022}/C_{2019} = 0.663$, $N_{2022}/N_{2019} = 0.695$, $P_{2022}/P_{2019} = 0.492$) in the plot where *C. gigantea* was investigated. In the plot where *M. candidum* was investigated, we found less pronounced differences between the locations under ALAN ($C_{2022}/C_{2019} = 0.677$, $N_{2022}/N_{2019} = 0.761$, $P_{2022}/P_{2019} = 0.729$) and those 10m away from ALAN ($C_{2022}/C_{2019} = 0.712$, $N_{2022}/N_{2019} = 0.746$, $P_{2022}/P_{2019} = 0.742$).

DISCUSSION

Our findings support the hypothesis that artificial light at night (ALAN) can influence leaf mass per area (LMA) in understory plants, but the response appears to vary among species. We observed a significant decrease in LMA in response to ALAN in shade-torelant species *Colocasia gigantea*, but not in light-demanding species *Melastoma candidum*.

We observed the apparent decline in soil nutrient content from 2019 to 2022. This trend could be primarily attributed to the nutrient absorption characteristics of the rubber trees (Yang et al. 2004) and the absence of fertilizer applications in our study site. Rubber trees are known for their high nutrient uptake, which can lead to significant soil nutrient depletion over time. This effect was evident in our study, with noticeable decreases in soil nutrient levels over two years in both ALAN-influenced and non-influenced areas. This soil nutrient decline seemed less pronounced near ALAN in the plot populated by *C. gigantea*. This trend suggests a potential positive impact of ALAN on soil nutrient content, likely mediated by the attraction of insects. ALAN is known to attract insects, which, upon death due to collision, overheating, or predation, could contribute additional nutrient inputs into the soil, such as N and P (Minnaar et al. 2015, Owens and Lewis 2018). This ALAN-induced insect influx could help offset the nutrient depletion caused by the nutrient-intensive rubber trees, thereby helping to maintain soil nutrient levels under ALAN exposure.

The significant decrease in LMA for *C. gigantea* under ALAN could be predominantly driven by indirect effects mediated through changes in soil nutrient availability rather than direct effects of ALAN acting as a light resource because sunlight increased LMA (Table 1). The presence of ALAN is known to attract a higher density of insects, many of which may die due to collision, overheating, dehydration, or predation (Minnaar et al. 2015, Owens and Lewis 2018). The decomposition of these deceased insects could lead to considerable enrichment of soil nutrients, particularly N and P (Schulze et al. 1997, Fagan et al. 2002, Woods et al. 2004, Behie and Bidochka 2013), which are fundamental to plant growth. Although the precise quantity of dead insects and the resultant increase in soil nutrient content is a subject for further detailed study, this enhanced nutrient availability could potentially shift the resource allocation strategy of *C. gigantea*. Additionally, increased soil nutrient availability, particularly N, could increase the photosynthetic capacity of *C. gigantea*. The enhanced nutrient availability may enable *C. gigantea* to allocate more resources to rapid leaf growth rather than structural tissue, leading to a decrease in LMA (Onoda et al. 2017, Hernández-Vargas et al. 2019).

On the other hand, ALAN did not have a significant effect on LMA in the light-demanding species *M. candidum*. light-demanding species receive stronger sunlight than shade-torelant species, which might result in the small effect of ALAN on their LMA. Because the effect of daylight was not significant either, intraspecific trait variability (ITV) itself for light-demanding species may inherently be smaller than for shade-torelant species. Although many studies have explored ITV within different functional groups, such as herbs and trees (Siefert et al. 2015), there needs to be more research into the ITV differences between light-demanding species and shade-torelant species. Additionally, the less pronounced soil nutrient differences between ALAN-influenced and non-influenced areas in the plot with *M. candidum* compared to the plot with *C. gigantea* may explain the lack of significant change in LMA for *M. candidum*. The ALAN treatment was set up on a slope in this plot, and therefore, increased soil nutrients resulting from dead insects attracted by ALAN might be more likely to be washed off and not persist in the soil (Zhao et al. 2013, Yi et al. 2018, Bai et al. 2020). Alternatively, ALAN's attraction to insects might be spatially dependent, which leads to certain locations attracting fewer insects and consequently experiencing a diminished soil fertilization effect.

ALAN, an increasingly prevalent aspect of our anthropogenic world, can have complex and nuanced impacts on forest ecosystems. Although it has been demonstrated that insolation (i.e., natural light) increases LMA (Ackerly et al. 2002, Niinemets et al. 2004), our research indicates that ALAN may influence LMA more indirectly by enhancing soil nutrient availability rather than directly acting as a light resource. ALAN may unexpectedly impact forest health and productivity by affecting understory plant functional traits and possibly soil nutrient dynamics. Controlled experiments potentially underestimate species interactions and unpredictable environmental heterogeneity because many irreplaceable features of field conditions, such as subtle nutrient change, herbivores, and competitors, are usually absent in the controlled experiments. Thus, robust tests of the ALAN effects on the understory will require more experimental work under field conditions. Further investigations into the intricate relationships between ALAN, plant functional traits, and soil nutrient dynamics are warranted to enable the development of comprehensive forest management strategies that consider the broad implications of artificial lighting.

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AUTHOR CONTRIBUTIONS

C.Z. and M.K. conceived the study; A.N. and X.S. set up the ALAN expreiment; C.Z. and X.S. collected data; C.Z. performed the analysis; C.Z. and M.K. led the writing of the paper; and all authors contributed to revisions.

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Fig. 1: Photographs of the experimental setup during daytime (A) and nighttime (B) in a rubber tree forest within the Xishuangbanna Tropical Botanical Garden (XTBG), China. One of the target species, *Colocasia gigantea*, is visible in both pictures.

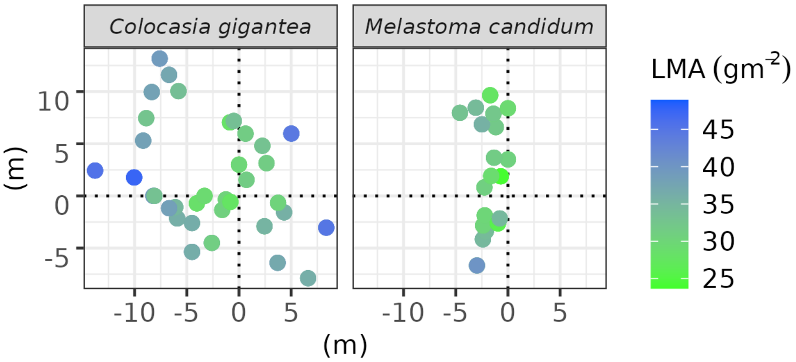

Fig. 2: Leaf mass per area (LMA) values of individuals from the two experimental species, *C. gigante* and *M. candidu*, in realtion to their relative geographic locations with respect to the artificial light at night (ALAN). The ALANs are located in the center of the maps (0, 0). Color represents the LMA values.

Table. 1. Summary of Bayesian linear mixed-effect models testing the effects of artificial light at night (ALAN), daylight, and their interaction on leaf mass per area (LMA) values. Posterior means and 95% credible intervals (CI) are shown. Intervals that do not include zero are highlighted in bold.

Variables	Mean	95% CI
Melastoma candidum		
ALAN	-0.0434	[-0.1147, 0.0278]
Daylight	0.0006	[-0.0736, 0.0768]
ALAN × Daylight	-0.0309	[-0.0840, 0.0233]
Colocasia gigantea		
ALAN	-0.1052	**[-0.1500, -0.0613]**
Daylight	0.0489	**[0.0036, 0.0934]**
ALAN × Daylight	-0.0113	[-0.0436, 0.0216]