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Research Article

# Artificial Light at Night (ALAN) Influences Growth, Physiological, and Metabolite Profiles in Mahogany Seedlings (*Swietenia macrophylla* King)

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## ABSTRACT

Light is essential for plant life, as it influences growth, physiology, and metabolism. Artificial Light at Night (ALAN), commonly used for recreational purposes, such as in the Bogor Botanical Garden (Kebun Raya Bogor/KRB) from December 2021 to October 2022, may have an adverse effect health of tropical plants. However, its impacts on tropical tree species, such as mahogany (*Swietenia macrophylla* King), remains poorly understood. This study aims to investigate the effects of ALAN on mahogany seedlings by assessing their growth performance, physiological responses, and changes in metabolite profile under various ALAN treatments. A split-plot factorial randomised block design with three replications was employed. The treatments comprised three ALAN factors: light colour, duration, and intensity. Parameters measured included growth rate, photosynthetic rate, chlorophyll content, and metabolite profiles. The results indicated that ALAN significantly increased chlorophyll content, but decrease stomatal conductance, transpiration, and photosynthethic rate, leading to reduced growth. Moreover, ALAN altered secondary metabolism, with decrease in several flavonoids (e.g., cyanidin, phellopterin, and homoorientin) and increase in salicylic acid, jasmonic acid, and astilbin.These findings highlighted the detrimental effects of ALAN on tropical plants and provided valuable insights for managing agroforestry systems and urban green spaces.



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## INTRODUCTION

Plants rely on specific light wavelengths during the day and darkness at night to regulate their life processes (Singhal et al. 2019). The rise of Artificial Light at Night (ALAN) over the past century, driven by urbanisation and technological advancements, has raised concerns about its environmental impact on plants (Speiber et al. 2021). ALAN originates from various sources, including streetlights, floodlights, illumination building, security lighting, household lights, and vehicle headlights (Gaston et al. 2015). Despite its social and economic benefits, the effects of ALAN on plants are increasingly troubling.

ALAN disrupts light cycles, affecting plant circadian rhythms, productivity, and morphology, including growth rates, leaf area, and biomass (Bennie et al. 2016; Speiber et al. 2021). It increases Reactive Oxygen Species (ROS) production, weakening plant resistance to stress (International Dark-Sky Association 2022). Over time, ROS accumulation causes metabolic disorders, disrupting photosynthesis and metabolite synthesis (Kwak et al. 2018; Satria et al. 2021). ALAN also impacts broader ecological processes, including pollination, flowering, food webs, microhabitats, and the evolution of plant species (Singhal et al. 2019). It is recognised as a global environmental challenge due to its effects on biodiversity (Falcon et al. 2020). Therefore, ALAN requires careful assessment, especially in urban and rural areas, as well as plant conservation zones.

Most studies on ALAN's impact have focused on subtropical regions. A 40-month research using high-pressure sodium lamps reported significant changes in photosynthetic pigment composition, leading to a reduction in the photosynthetic rates and biomass in Yellow Poplar (*Liriodendron tulipifera* L.) seedlings (Kwak et al. 2018). Similarly, urban plants such as *Euonymus japonicus* and *Rosa hybrida* exhibited decreased gas exchange rates, photosynthetic pigments, and photosynthesis under red and blue ALAN exposure, along with stress-related metabolic changes such as increased malondialdehyde and sugar levels (Wei et al. 2023). High-intensity ALAN further suppressed photosynthesis and respiration in both species (Wei et al. 2024). However, the impact of ALAN on tropical species, particularly in conservation areas like the Bogor Botanical Garden (Kebun Raya Bogor/KRB), remains underexplored.

KRB, an ex-situ plant conservation site in Indonesia, houses a diverse collection of tropical plant species, including mahogany (*S. macrophylla* King), which must be protected from biotic and abiotic disturbances (Firmansyah et al. 2022), including ALAN. As a heliophilic species, *S. macrophylla* thrives in sunlight, tolerates high temperatures, and adapts to various environments, making it well-suited for use as an urban shade tree (Grogan et al. 2005; Larekeng et al. 2019). It also plays a vital role in agroforestry systems, contributing to reforestation efforts and enhancing soil quality (Mashudi et al. 2016). Beyond its ecological significance, *S. macrophylla* possesses economic and medicinal value, as it contains bioactive compounds used in industrial and pharmaceutical applications (Borah et al. 2023), yet remains vulnerable to overexploitation and illegal trade.

*S. macrophylla* has been classified as Vulnerable since 1998 and was upgraded to Endangered in 2023 due to population declines and habitat loss (Barstow & Negrao 2023). As threats to the species continue to rise, urgent conservation measures are increasingly necessary. While deforestation and illegal logging have been widely studied, the impact of ALAN on its survival and physiology remains unexamined. This study investigated the effects of ALAN on the growth, physiological responses, and metabolite composition of *S. macrophylla* seedlings under various light conditions. The findings provided insights into ALAN's impact on tropical plants and supported conservation strategies for managing artificial lighting in urban and conservation areas like the Bogor Botanical Garden.

## MATERIALS AND METHODS

### Materials

The primary material used in this study was 1-year-old *S. macrophylla* seedlings from the IPB Nursery Garden, selected for their uniform height and leaf number. Additional materials include acetone (Merck, Germany) and ethanol (Merck, Germany). Equipment used consists of a 20 W RGB LED spotlight (Hitato, China), LI-COR 6400XT (LI-COR Inc., USA), grinder blender (Miyako BL-101 GS, Indonesia), oven (Memmert UN 450, Germany), LC-MS instrument UHPLC Vanquish Tandem Q Exactive Plus Orbitrap HRMS (Thermo Scientific, USA), SP-UV1100 spectrophotometer (Dlab, China), centrifuge (Heraeus Labofuge 400R, Germany), digital scale (Precisa XT 6200C, Switzerland), and tape measure (Butterfly, China).

### Methods

#### Experimental Design

The study employed a split plot factorial randomised group design with 3 replications, each consisting of one seedling. Treatment involved three factors: light colour (red, green, and blue) as the main plot, light duration as the sub-plot (1h/2n, 1h/7n, 6h/2n, 6h/7n, 12h/2n, 12h/7n)), and light intensity as the sub-sub-plot (high and low) (Table 1). The selection of light colours and exposure durations was based on settings used in night tourism activities at KRB, typically conducted twice per week. A 6-hour exposure applied twice per week (6h/2n) was designed as the reference treatment. Additional durations were designed to simulate shorter exposure (1 hour), longer exposure (12 hours), and more frequent application (7 nights per week) relative to the reference. Light intensity was measured using a lux meter, and the average high and low values differed among colours: red (75.83 and 16.65 lux), green (62.07 and 15.93 lux), and blue (37.42 and 7.52 lux).

#### Treatments

ALAN treatments were applied from June 2023 to June 2024. Samples were arranged on 19 experimental racks spaced 100 cm apart. Each rack, constructed from lightweight steel frames, measured 120 × 120 × 230 cm (length × width × height). The rack had two levels, with three plants placed on each level, giving a total of six plants per rack. Low-intensity ALAN was applied to plants on the lower level, with an initial distance of approximately 100 cm between the light source and the canopy. High-intensity ALAN was applied to plants on the upper level, where the initial distance was about 50 cm. Lights were switched on at 7:00 PM for the 1 and 6-hour treatments and at 6:00 PM for the 12-hours treatment. Control plants were placed on racks without artificial night lighting, enabling them to undergo a 12-hours dark period at night.

#### Growth rate measurement

Growth measurements included plant height, leaf area, fresh and dry biomass of *S. macrophylla* at 12 months after treatment (MAT). Plant height was measured from the soil surface to the tip of the plant. Leaf area was determined using scanned leaf images and ImageJ software. Fresh weights of roots and crowns was recorded before drying at 60 °C to obtain dry biomass.

#### Photosynthesis, transpiration rate, and stomatal conductance measurement

Measurements were taken using an LI-COR 6400 on mature leaves of *S. macrophylla* at 3, 6, 9, and 12 MAT. All Measurements were conducted on clear days between 09:00 and 11.00 AM under the chamber conditions: photosynthetically active radiation (PAR) set at 1000 µmol $m^{-2}$ $s^{-1}$, leaf temperature at 30 °C, relative humidity at 60 %, and $CO_2$ concentration at 400 ppm. Before

**Table 1.** Factors, levels, and treatment codes used in the study of ALAN effects on *Swietenia macrophylla* seedlings.

| Light colour | Light intensity | Light duration | Treatment code |
|---|---|---|---|
| Control | - | - | - |
| Red | High | 1 hour over 2 nights | RH-1h/2n |
| | Low | | RL-1h/2n |
| | High | 1 hour over 7 nights | RH-1h/7n |
| | Low | | RL-1h/7n |
| | High | 6 hours over 2 nights | RH-6h/2n |
| | Low | | RL-6h/2n |
| | High | 6 hours over 7 nights | RH-6h/7n |
| | Low | | RL-6h/7n |
| | High | 12 hours over 2 nights | RH-12h/2n |
| | Low | | RL-12h/2n |
| | High | 12 hours over 7 nights | RH-12h/7n |
| | Low | | RL-12h/7n |
| Green | High | 1 hour over 2 nights | GH-1h/2n |
| | Low | | GL-1h/2n |
| | High | 1 hour over 7 nights | GH-1h/7n |
| | Low | | GL-1h/7n |
| | High | 6 hours over 2 nights | GH-6h/2n |
| | Low | | GL-6h/2n |
| | High | 6 hours over 7 nights | GH-6h/7n |
| | Low | | GL-6h/7n |
| | High | 12 hours over 2 nights | GH-12h/2n |
| | Low | | GL-12h/2n |
| | High | 12 hours over 7 nights | GH-12h/7n |
| | Low | | GL-12h/7n |
| Blue | High | 1 hour over 2 nights | BH-1h/2n |
| | Low | | BL-1h/2n |
| | High | 1 hour over 7 nights | BH-1h/7n |
| | Low | | BL-1h/7n |
| | High | 6 hours over 2 nights | BH-6h/2n |
| | Low | | BL-6h/2n |
| | High | 6 hours over 7 nights | BH-6h/7n |
| | Low | | BL-6h/7n |
| | High | 12 hours over 2 nights | BH-12h/2n |
| | Low | | BL-12h/2n |
| | High | 12 hours over 7 nights | BH-12h/7n |
| | Low | | BL-12h/7n |

Note: Treatment codes were adjusted according to the interacting factors. If only two factors interacted, the code represents those two factors. R: Red, G: Green, B: Blue; H: High intensity, L: Low intensity. Duration is expressed as h: hour per n: night/week.

recording, leaves were allowed to stabilise in the chamber for 2-3 minutes until gas exchange parameters reached steady state. Three replicate measurements were taken per seedling.

### Chlorophyll content measurement

Total chlorophyll content of *S. macrophylla* was measured at 12 MAT using the method of Lichtenthaler et al. (1981) at wavelengths (λ) = 663 and 646 nm. 0.1 g mature leaf samples were extracted with 10 ml of 80 % acetone. The total chlorophyll content was determined based on the formula:

$$\text{Chlorophyll a} = 12.25 \times A_{663} - 2.79 \times A_{646}$$

$$\text{Chlorophyll b} = 21.50 \times A_{646} - 5.10 \times A_{663}$$

$$\text{Total chlorophyll} = (7.15 \times A_{663}) + (18.71 \times A_{646})$$

### Secondary metabolite profile analysis

Metabolite analysis was performed at 12 MAT on control plants and several treatment that exhibited varying degrees of growth and physiological effects RL-1h/7n, RL-6h/7n, RH-6h/7n, GL-1h/7n, GL-6h/7n, GH-6h/7n, BL-1h/7n, BL-6h/7n, BH-6h/7n (Table 1). Leaf extraction followed Hita et al. (2022), using 20-30 mature leaves per treatment. Leaves were washed, dried at 45 °C for two weeks, and pulverised . Three grams of powder were soaked in 30 ml of 70 % ethanol and incubated at 120 rpm using a shaker for 72 hours. The extract was filtered using Whatman No. 1 filter paper, evaporated with a rotary evaporator at 50˚C, and analysed at the Advanced Laboratory, IPB University. 2 µL sample (10 mg $mL^{-1}$) was injected into an LC-MS system using an Accucore C18 column (100 x 2.1 mm, 1.5 µm) with a flow rate of 0.2 mL $min^{-1}$ and a column temperature of 30 °C. The mobile phase consisted of water with 0.1 % formic acid (A) and acetonitrile with 0.1 % formic acid (B), with gradients set as: 0-1 min (5 % B), 1-25 min (5-95 % B), 25-28 min (95 % B), and 28-35 min (5 % B). Mass spectrometry was performed with electrospray ionisation in positive and negative modes, scanning from 100-1500 m/z, with conditions set as: capillary temperature 320 °C, sheath gas flow rate 15 µm $min^{-1}$, auxiliary gas flow rate 3 L $min^{-1}$, spray voltage 3.8 kV, and S-lens RF level 50.

### Data analysis

Growth and physiology data were analysed using Rstudio software, with significance tested by Analysis of Variance (ANOVA) at a 95 % confidence level. Significant differences were analysed using the Duncan Multiple Range Test (DMRT) at $\alpha = 5$ %. Metabolomic data were analysed using the Mzmine (Schmid et al. 2023) and MetaboAnalyst 6.0 (https://www.metaboanalyst.ca/) for heatmap construction. Metabolite identification was conducted using the PubChem database (https://pubchem.ncbi.nlm.nih.gov/) and MassBank of North America (https://mona.fiehnlab.ucdavis.edu/).

## RESULTS AND DISCUSSION

*S. macrophylla* grows optimally in tropical regions, where it experiences an equal 12-hour light and dark period (Snook 2000). The dark period at night is essential for key physiological processes, including respiration, energy storage, cell recovery and repair, and the maintenance of overall physiological balance (Cheng et al. 2019). The presence of ALAN during the dark period significantly affected all observed growth and physiological variables of *S. macrophylla* seedlings in this study.

ALAN increased chlorophyll biosynthesis in *S. macrophylla* seedlings (Figure 1), likely because the plant misinterpreted nighttime ALAN as shaded conditions (Segrestin et al. 2021), thereby triggering an adaptive increase in chlorophyll to enhance light absorption (Wei et al. 2024). Total chlorophyll content was significantly affected by the interaction between light duration and intensity ($p<0.05$), with L-6h/7n exhibiting the highest content (Figure 1A). Light type also had a significant effect ($p<0.05$), particularly under blue light (Figure 1B), which is known to regulate stem elongation, pigment accumulation, biomass production, and photosynthesis (Ouzounis et al. 2015). Blue light enhances chloroplast development and function through photoreceptors such as cryptochromes and phototropins, and it influences the circadian clock and chlorophyll biosynthesis (Bennie et al. 2016). Comparable increases were observed in *Liriodendron tulipifera* after one year of ALAN exposure (Kwak et al. 2018).

High chlorophyll levels do not necessarily correlate with higher photosynthetic rates (Cho et al. 2024). Despite the increase in chlorophyll content,

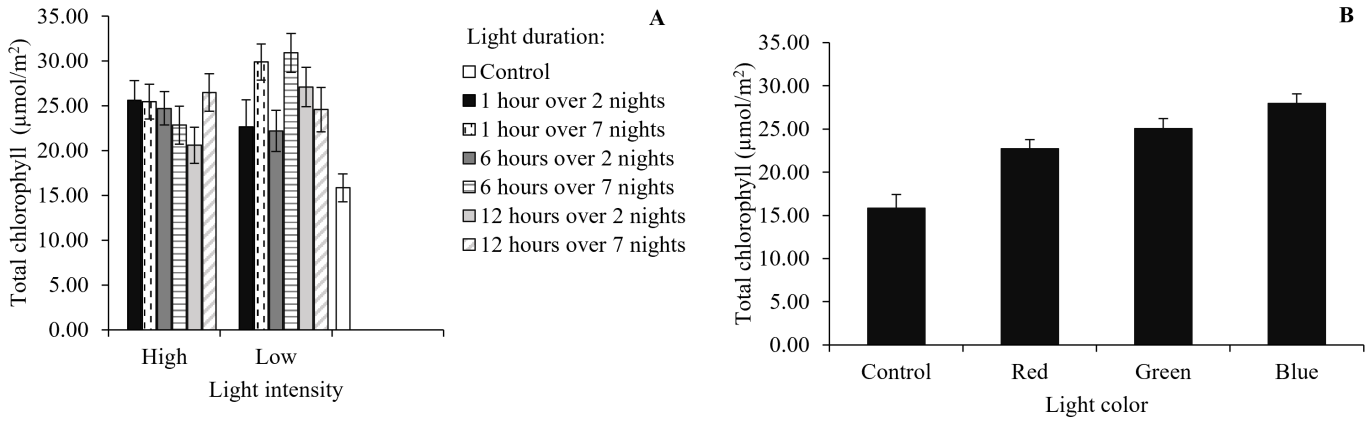


**Figure 1.** Total chlorophyll content of *Swietenia macrophylla* affected by ALAN after 12 months treatment, with an interaction between different light intensity and duration (A) and light colour (B) treatments. Data are presented as means (n=3) ± SE.

*S. macrophylla* seedlings exposed to ALAN exhibited lower photosynthesis rates, particularly at 9 and 12 MAT (Figure 2). ALAN disrupts circadian rhythms, impairing the regulation of photosynthesis and disturbing the balance between light and dark reactions, which results in inefficient energy utilization and excessive ROS accumulation. Elevated ROS can damage photosynthetic components, thereby reducing efficiency and slowing photosynthetic rate (Kwak et al. 2018).

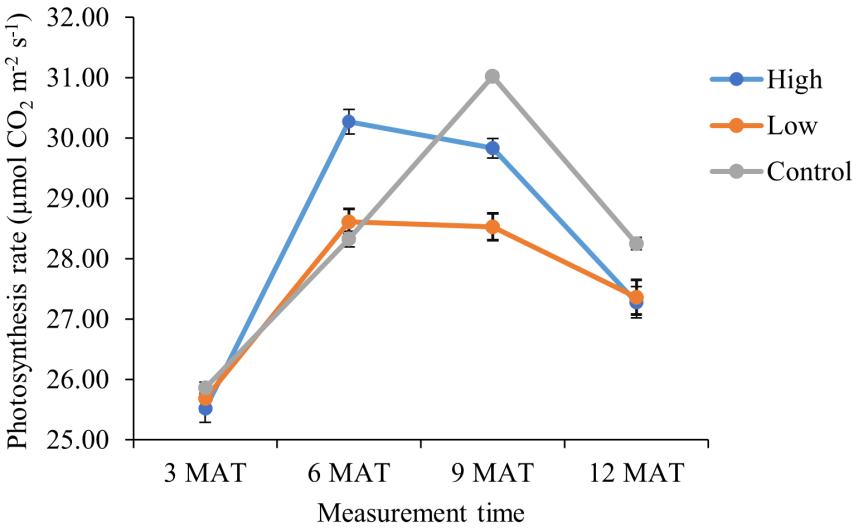


**Figure 2.** The Photosynthesis rate of *Swietenia macrophylla* was affected by ALAN under high and low light intensities at 3, 6, 9, and 12 months after treatment. Data are presented as means (n=3) ± SE.

The success of photosynthesis is strongly influenced by environmental light intensity. The ALAN intensities used in this study (7–37 lux) were below the minimum threshold required to optimally support photosynthetic reactions. Bennie et al. (2016) reported that night-time light pollution (skyglow; 0.1–0.5 lux) may slightly induce photosynthetic responses, but effective carbon fixation occurs only when leaves are very close to the light source, such as directly beneath street lamps (50 lux) or vehicle headlights, which can reach several thousand lux. In this study, *S. macrophylla* seedlings exposed to low-intensity ALAN exhibited lower photosynthetic rates than those under high-intensity ALAN (Figure 2). This response is likely attributable to the heliophilic nature of mahogany, which enables more efficient energy utilization under relatively high light intensities compared to its normal growth

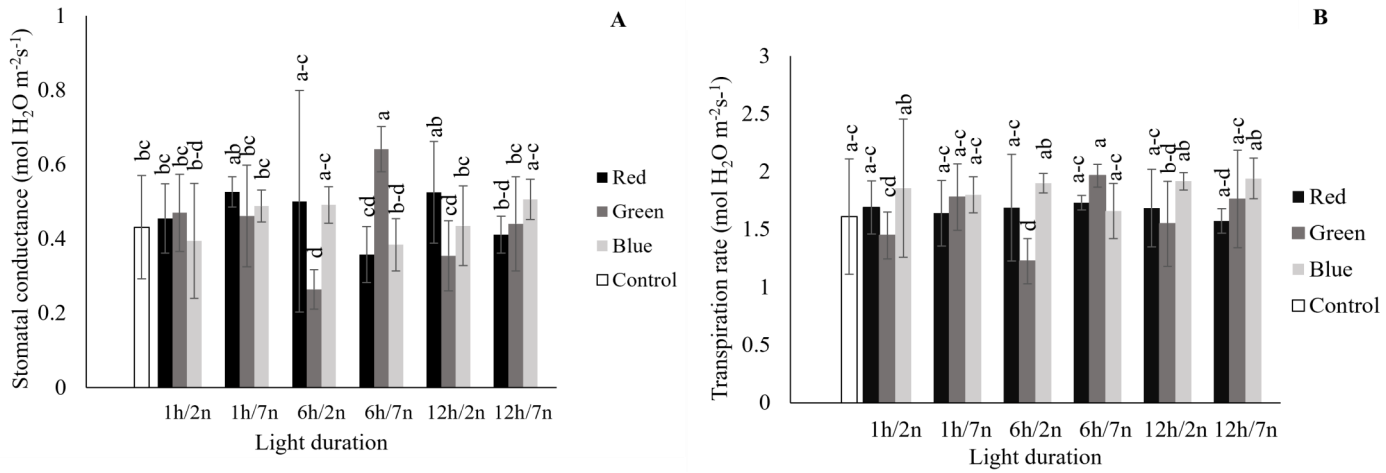


**Figure 3.** Stomatal conductance (A) and transpiration rate (B) of *Swietenia macrophylla* affected by ALAN after 12 months treatment, with an interaction between different light colour and duration. Data are presented as means (n=3) ± SE.

conditions (Goncalves et al. 2007).

The reduction in photosynthetic rate under ALAN stress may also be influenced by stomatal factors (Wei et al. 2023), including stomatal conductance and transpiration rate. These factors strongly affect photosynthesis under ALAN stress, as stomatal conductance regulates both water vapor loss and $CO_2$ uptake. Reduced stomatal conductance, as observed in H-6h/2n, limits transpiration by lowering the humidity gradient between the leaf interior and the surrounding air (Figure 3) (Guerrieri et al. 2019; Lv et al. 2024). This, in turn, decreases $CO_2$ diffusion into leaves, thereby suppressing photosynthetic activity (Kim & Lieth 2003; Lv et al. 2024). Thus, although increased chlorophyll levels may enhance light-harvesting capacity, reduced stomatal conductance and transpiration constrain $CO_2$ assimilation, ultimately resulting in lower photosynthetic rates under ALAN exposure. The reduction in photosynthesis under ALAN not only limited energy capture but also restricted carbon availability for secondary metabolite biosynthesis, thereby explaining the observed declines in several compounds.

Several secondary metabolites exhibited a significant decrease in concentration ($p<0.05$) or a Variable Importance in Projection (VIP) value greater than 1 under all ALAN treatments, including cyanidin, homoorientin, and phellopterin (Figure 4). As shown in the heatmap (Figure 5), the concentrations of these compounds were highest in the control plants (red on the scale), whereas all ALAN treatments resulted in a decreased levels (blue on the scale).

Cyanidin, an anthocyanin, is responsible for the reddish colouration of young leaves (Gould 2004). Cyanidin and other anthocyanins are highly sensitive to environmental factors such as ALAN, which led to the greatest reduction in concentration and correspondingly high VIP values (Figure 4). ALAN may disrupt the circadian regulation of anthocyanin biosynthesis genes. Enzymes such as β-glucosidase hydrolyse glycosidic bonds in anthocyanins, converting them into colourless chalcones, while polyphenol oxidase catalyses the oxidation of phenolic compounds, thereby accelerating anthocyanin degradation (Ifadah et al. 2021). Furthermore, cyanidin degradation and reduced accumulation are also associated with ALAN-induced oxidative stress. Cyanidin, which possesses strong antioxidant and photoprotective properties, declines in concentration as it is consumed in protecting plants against oxidative stress and damage caused by UV radiation and other light-related stressors (Gould 2004; Mattioli et al. 2020; Li & Ahammed 2023).

Homoorientin and phellopterin also showed significant reductions un-

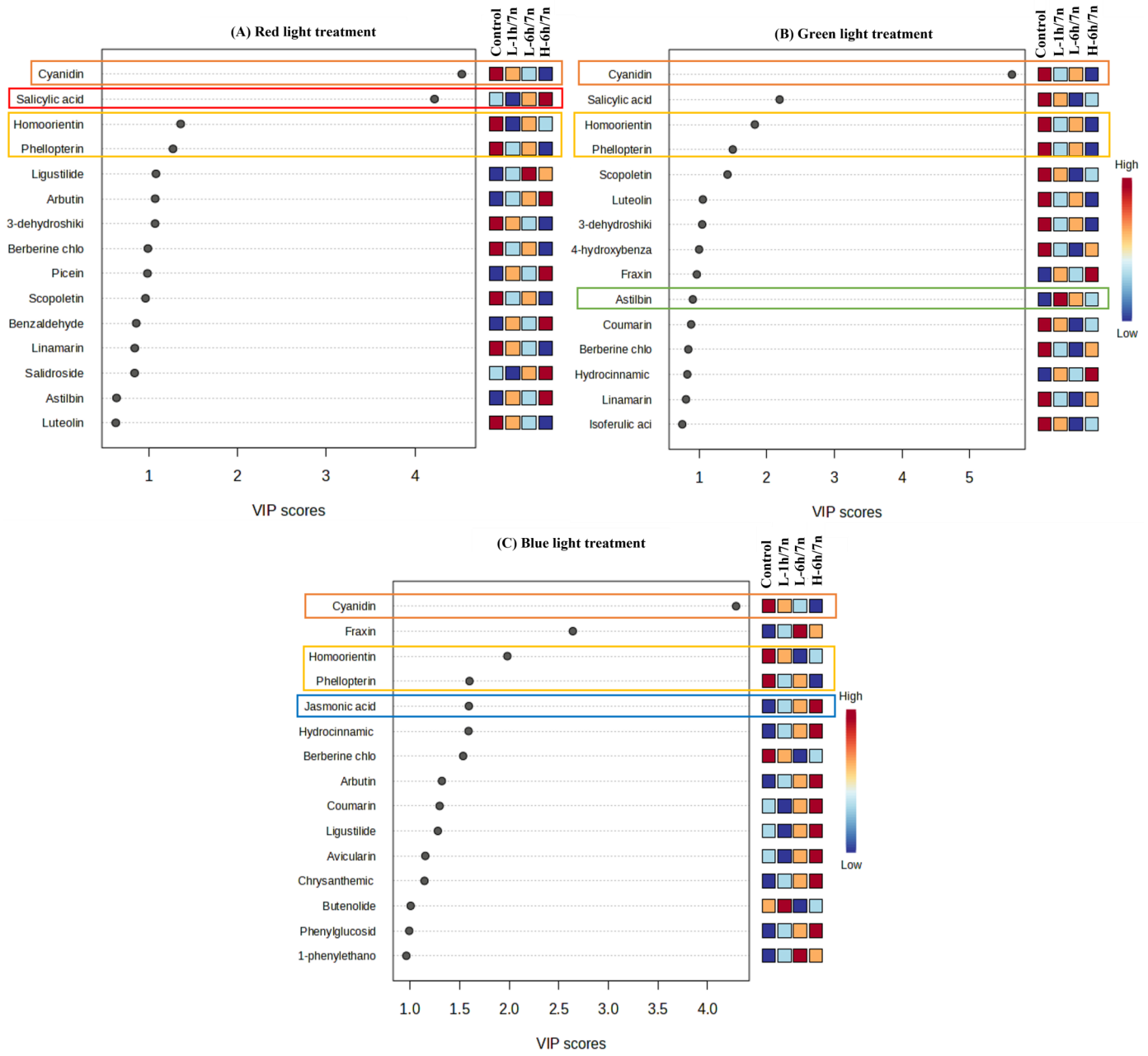


**Figure 4.** Variable Importance in Projection (VIP) scores of metabolites in *Swietenia macrophylla* after 12 months of ALAN treatment. H: high intensity, L: low intensity. Duration is expressed as h: hour per n: night/week.

der all ALAN treatments (Figure 4 and Figure 5). Both compounds possess antioxidant activity and contribute to plant defence against abiotic stresses, including ALAN (Zielinska & Zielinski 2011; Lamichhane et al. 2023). These metabolites, along with most others that declined under ALAN, belong to the flavonoid group.

Flavonoids play diverse roles in plants, functioning as signalling molecules, detoxifying agents, regulators of growth, modulators of temperature acclimation, and scavengers of ROS generated by UV radiation (Roy et al. 2022). Typically localised in the epidermis and hypodermis, flavonoids act as protective barriers, preventing UV radiation from penetrating deeper tissues (Mierziak et al. 2014). The spectral composition, intensity, and duration of ALAN can alter the expression of genes involved in flavonoid biosynthesis, thereby affecting their concentration (Fonseca et al. 2023). A reduction in flavonoid content may indicate that these compounds are being consumed to mitigate ALAN-induced oxidative stress, allowing plants to sustain daytime physiological functions. However, suppressed flavonoid biosynthesis could

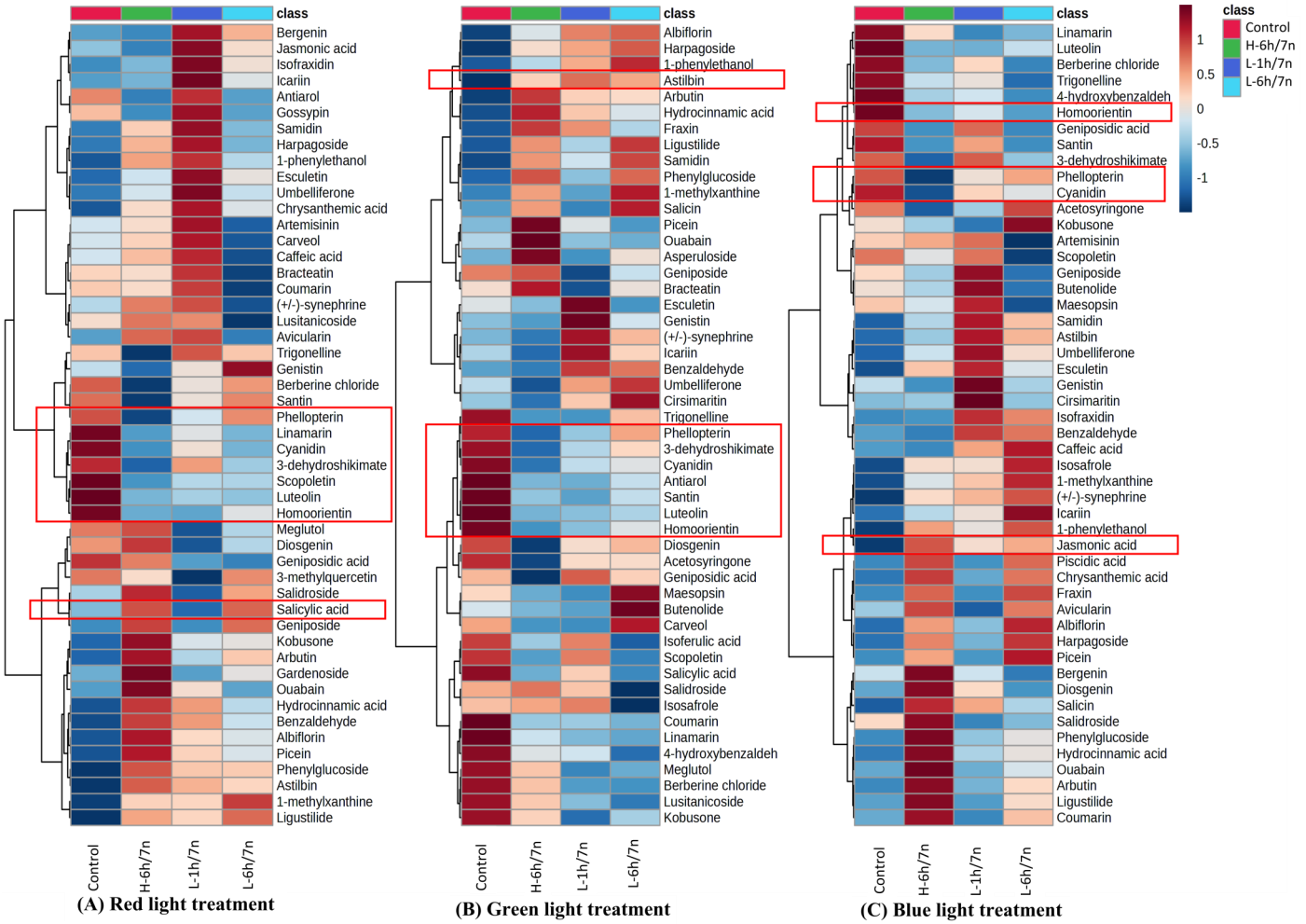


**Figure 5.** Heatmap of the secondary metabolite profile of *Swietenia macrophylla* affected by ALAN at 12 months after treatment. H: high intensity, L: low intensity. Duration is expressed as h: hour per n: night/week.

render plants more vulnerable to light stress due to diminished protective capacity. Furthermore, as the biosynthesis of key secondary metabolites decreased under carbon limitation, less carbon was allocated to structural growth, ultimately reducing overall growth performance under ALAN exposure.

The growth of *S. macrophylla* seedlings exposed to ALAN was slower than that of those not exposed, as indicated by reduced plant height, leaf area, and biomass. Plant height was significantly affected by the interaction of ALAN factors (colour, duration, and intensity) ($p<0.05$), with the BL-12h/7n treatment causing the greatest reduction (Table 2). Leaf area and plant biomass were independently influenced by light intensity and duration ($p<0.05$), with high-light intensity and the 12h/7n duration leading to the most significant declines (Figure 6A and 6B). Seedlings exposed to low-intensity ALAN had lower total fresh and dry biomass than the controls (Table 3), with the 6h/7n treatment resulting in the lowest values (Table 4).

Continuous ALAN treatments (1h/7n, 6h/7n, 12h/7n) resulted in reduced plant height, smaller leaf area, and lower plant biomass compared to non-continuous treatments (1h/2n, 6h/2n, 12h/2n) (Table 2, Figure 6B, Table 4). Periodic ALAN allowed dark periods that supported cell recovery and growth (Lagisz & Lagisz 2023), whereas continuous exposure disrupted circadian rhythms essential for physiological regulation (Friulla & Varone 2025), potentially leading to maladaptive growth. Notably, the 6h/7n and 1h/7n treatments caused greater biomass reduction than the 12h/7n treatment (Table 4), possibly because shorter ALAN durations did not provide sufficient stability for adaptation. In contrast, the consistent 12-hour exposure may

**Table 2**. Canopy height increase (cm) of *Swietenia macrophylla* affected by ALAN at 12 months after treatment.

| Treatment | Red (R) | | Green (G) | | Blue (B) | |
|---|---|---|---|---|---|---|
| | High (H) | Low (L) | High (H) | Low (L) | High (H) | Low (L) |
| Control | 9.79$^{a}$ | 9.79$^{a}$ | 9.79$^{a}$ | 9.79$^{a}$ | 9.79$^{a}$ | 9.79$^{a}$ |
| 1h/2n | 6.79$^{b-d}$ | 4.48$^{j-m}$ | 5.64$^{b-k}$ | 4.67$^{h-m}$ | 5.91$^{b-i}$ | 5.15$^{d-k}$ |
| 1h/7n | 5.36$^{c-k}$ | 4.55$^{i-m}$ | 5.55$^{b-k}$ | 6.09$^{b-h}$ | 5.03$^{e-l}$ | 4.88$^{f-l}$ |
| 6h/2n | 5.97$^{b-i}$ | 4.76$^{g-m}$ | 6.15$^{b-g}$ | 5.52$^{c-k}$ | 5.97$^{b-j}$ | 6.97$^{bc}$ |
| 6h/7n | 6.00$^{b-i}$ | 6.64$^{b-e}$ | 5.12$^{d-k}$ | 3.88$^{lm}$ | 6.76$^{b-d}$ | 4.42$^{k-m}$ |
| 12h/2n | 5.85$^{b-j}$ | 7.33b$^{b}$ | 5.79$^{b-j}$ | 4.70$^{h-m}$ | 6.48$^{b-f}$ | 6.58$^{b-e}$ |
| 12h/7n | 6.67$^{b-e}$ | 5.27$^{d-k}$ | 6.03$^{b-i}$ | 6.58$^{b-e}$ | 7.03$^{bc}$ | 3.70$^{m}$ |

Note Values followed by different letters within each treatment unit indicate significant differences based on the DMRT test ($p<0.05$). Data were transformed using log 10(x). Values represent the means of n=3. Duration is expressed as h: hour per n: night/week.

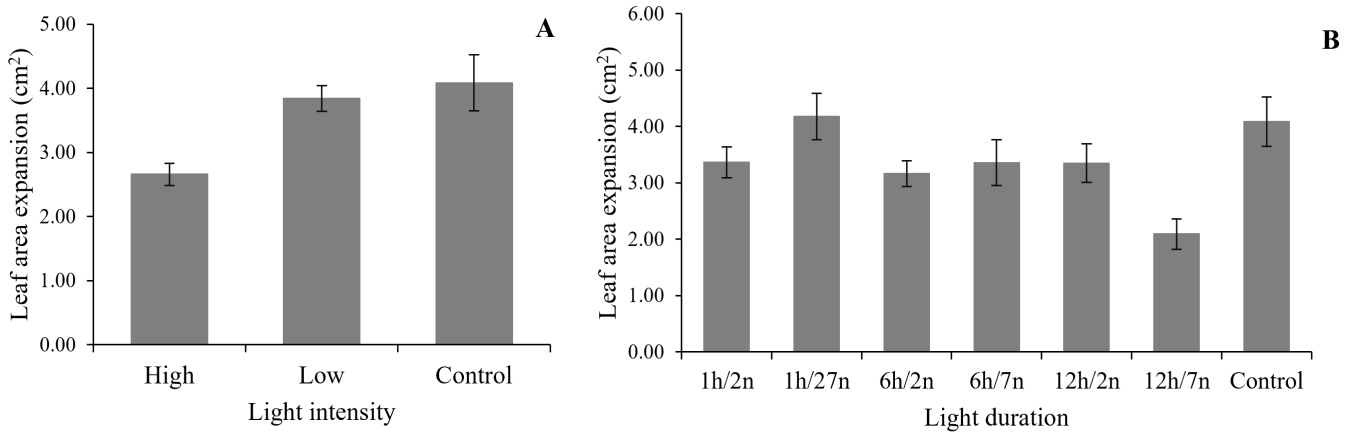


**Figure 6.** Leaf area expansion of *Swietenia macrophylla* affected by ALAN under different light intensity (A) and light duration (B) at 12 months after treatment. Duration is expressed as h: hour per n: night/week. Data are presented as means (n=3) ± SE.

have promoted stress tolerance (Wei et al. 2024).

ALAN exposure disrupts natural plant signaling processes that regulate biological functions at night (Falcon et al. 2020), affecting circadian rhythm gene expression and altering oscillatory patterns (Bennie et al. 2016). This disruption reduces energy capture and utilisation leading to metabolic imbalances and slower photosynthesis rates, which ultimately hinder plant growth (Giavi et al. 2021). Under ALAN-induced stress, carbon allocation shifts from growth to defence (Cao et al. 2024), resulting in shorter plant height, smaller leaf area, and lower total plant biomass in *S. macrophylla* seedlings compared with controls. Consistent with this metabolic reallocation, several defence-related metabolites increased under ALAN exposure suggesting an adaptive adjustment to mitigate stress.

Heatmap profiling revealed spectrum-dependent metabolic responses in *S. macrophylla* seedlings, with each ALAN colour treatment inducing a significant increase ($p<0.05$) in certain metabolites (red on the scale), in contrast to the consistently lower levels observed in the control plants (blue on the scale) (Figure 5). Among the metabolites that increased significantly and may serve as biomarkers of ALAN stress, salicylic acid (SA) was markedly elevated under red-light treatment, with a VIP score >1 (Figure 4A). According to (Yang et al. 2023), red light can trigger SA accumulation by activating phytochrome. Activated phytochrome induces CaHY5, a key transcription factor that regulates SA biosynthetic genes. SA is synthesised through the phenylpropanoid–benzoate pathway, via both the phenylalanine ammonia-lyase

**Table 3.** Plant biomass of *Swietenia macrophylla* affected by ALAN under different light intensities at 12 months after treatment.

| Light intensity | Plant fresh biomass (g) | | | Plant dry biomass (g) | | |
|---|---|---|---|---|---|---|
| | Root (A) | Shoot (B) | Total (A+B) | Root (C) | Shoot (D) | Total (C+D) |
| Control | 127.10$^{a}$ | 296.10$^{a}$ | 423.20$^{a}$ | 72.16$^{a}$ | 146.19$^{a}$ | 218.35$^{a}$ |
| High | 110.40$^{a}$ | 236.48$^{b}$ | 346.88$^{b}$ | 68.43$^{a}$ | 119.13$^{ab}$ | 187.56$^{a}$ |
| Low | 67.00$^{b}$ | 190.91$^{b}$ | 257.90$^{c}$ | 41.74$^{b}$ | 88.32$^{b}$ | 130.06$^{b}$ |

Note: Numbers followed by different letters in the same column indicate significant differences based on the DMRT test ($p<0.05$). Values represent the means of n=3.

**Table 4.** Plant biomass of *Swietenia macrophylla* affected by ALAN under different light durations at 12 months after treatment.

| Light duration | Plant fresh biomass (g) | | | Plant dry biomass (g) | | |
|---|---|---|---|---|---|---|
| | Root (A) | Shoot (B) | Total (A+B) | Shoot (C) | Root (D) | Total (C+D) |
| Control | 127.10$^{a}$ | 296.10$^{a}$ | 423.20$^{a}$ | 72.16$^{a}$ | 146.19$^{a}$ | 218.35$^{a}$ |
| 1h/2n | 95.51$^{b}$ | 230.32$^{b}$ | 325.83$^{b}$ | 58.84$^{b}$ | 112.53$^{b}$ | 171.37$^{b}$ |
| 1h/7n | 85.59$^{b}$ | 200.21$^{bc}$ | 285.81$^{bc}$ | 54.45$^{bc}$ | 96.52$^{bc}$ | 150.96$^{b}$ |
| 6h/2n | 89.89$^{b}$ | 219.69$^{b}$ | 309.58$^{b}$ | 55.81$^{bc}$ | 105.51$^{b}$ | 161.32$^{b}$ |
| 6h/7n | 74.04$^{b}$ | 174.87$^{c}$ | 248.91$^{c}$ | 43.86$^{c}$ | 78.61$^{c}$ | 122.48$^{c}$ |
| 12h/2n | 98.51$^{b}$ | 226.05$^{b}$ | 324.56$^{b}$ | 63.60$^{ab}$ | 115.25$^{b}$ | 178.85$^{b}$ |
| 12h/7n | 88.66$^{b}$ | 231.02$^{b}$ | 319.68$^{b}$ | 53.95$^{bc}$ | 113.92$^{b}$ | 167.87$^{b}$ |

Note: Numbers followed by different letters in the same column indicate significant differences based on the DMRT test ($p<0.05$). Duration is expressed as h: hour per n: night/week. Values represent the means of n=3.

and isochorismate pathways (Lefevere et al. 2020). Conversely, red-light signaling through CaHY5 suppresses the jasmonic acid (JA) pathway, which generally antagonistically to SA (Yang et al. 2023). Consequently, SA accumulation in mahogany suppresses JA production, particularly under RH-6h/7n and RL-6h/7n treatments (Figure 5).

Increased SA under ALAN stress induces ROS accumulation and its systemic propagation throughout the plant, thereby coordinating defence responses to both biotic and abiotic stresses. Although SA is classically associated with systemic acquired resistance (SAR) against pathogens, in the context of ALAN it can be considered a SAR-like defence, an analogous systemic adaptation triggered by abiotic stress (Fichman & Mittler 2020). SA enhances plant resistance by modulating endogenous signaling pathways, stimulating antioxidant enzyme activity, detoxifying superoxide radicals, preventing oxidative damage, and protecting cellular membranes and metabolic enzymes (Khan et al. 2015; Heinen et al. 2023).

In contrast to red light, blue ALAN exposure triggered a significant increase in jasmonic acid (JA) levels compared with the control, with a VIP score >1 (Figure 4C), thereby identifying JA as a potential stress biomarker under this light spectrum. JA is central to plant defence, stimulating antioxidant activity and the production of protective compounds that enhance stress resistance (Rehman et al. 2023). JA biosynthesis occurs via the oxylipin pathway, beginning with α-linolenic acid in chloroplasts and catalysed by lipoxygenase, allene oxide synthase, and allene oxide cyclase, producing 12-oxophytodienoic acid, which is subsequently converted to JA in peroxisomes (Mergová et al. 2023). JA is a key hormone in plant defence, typically associated with systemic wound responses (SWR) to herbivory or pathogen attack (Lee & Seo 2022). Similar to SA accumulation under red ALAN, JA elevation under blue ALAN may represent an SWR-like defence, an analogous systemic response triggered by abiotic stress (Fichman & Mittler 2020).

JA activates protective mechanisms by inducing antioxidant enzymes and defence-reated compounds, thereby helping to balance growth and stress

resistance (Rehman et al. 2023). JA signaling promotes the degradation of Jasmonate ZIM-domain (JAZ) proteins, which in turn activate MYC transcription factors. Together with DELLA proteins, MYCs suppress the biosynthesis of growth-related hormones, redirecting energy and metabolic resources toward the production of defence-associated metabolites and proteins (Huang et al. 2017).

*S. macrophylla* seedlings exposed to green ALAN exhibited a significant increase in astilbin concentration, with a VIP score >1 (Figure 4B), suggesting its potential role as a biomarker of ALAN stress under green light. Astilbin, a flavanonol glycoside, is synthesised through the rhamnosylation of taxifolin by glycosyltransferase (Petacci et al. 2010). As a potent antioxidant, astilbin scavenges ROS and mitigates ALAN-induced oxidative stress, thereby protecting cells and supporting sustained growth under unfavorable conditions (Dias et al. 2021; Yang & Zhang 2022).

The elevated levels of SA, JA, and astilbin in *S. macrophylla* seedlings exposed to ALAN can be considered early indicators of acclimation, as these metabolites play crucial roles in defence mechanisms and physiological adjustments to environmental stress (Wasternack & Strnad 2019; Lefevere et al. 2020; Yang & Zhang 2022). However, these responses reflect only short-term metabolic adjustments. To determine whether *S. macrophylla* can truly adapt or develop tolerance to ALAN, long-term observations extending to the generative phase are necessary to evaluate how these physiological and metabolic traits are inherited or subsequent generations (Jangpangi et al. 2025).

## CONCLUSIONS

ALAN stress likely disrupts *S. macrophylla* seedlings' circadian rhythms, reducing photosynthetic efficiency and trigerring physiological responses associated with oxidative stress. Changes in secondary metabolites, including a decline in flavonoids and altered levels of salicylic acid, astilbin, and jasmonic acid, suggested a compromised antioxidant defences system that is unable to fully mitigate ALAN-induced sress. Growth parameters such as plant height, leaf area, and biomass decreased significantly, indicating poor adaptation to prolonged exposure. The next research should investigate ALAN's impact on other plant species, particularly those frequently exposed to artificial lighting, and include direct measurements of ROS levels, longer durations, and additional environmental factors to better elucidate ALAN's long-term effects on plantphysiology.

## AUTHOR CONTRIBUTION

A.P.M. conducted the formal analysis, investigation, experiments, data collection and curation, original draft preparation, and visualization. M. and K.N.T. contributed to validation, provision of resources, data curation, and manuscript revision. F.D., K.N.T., and M.K.P. designed the study, conducted the experiments, and secured BRIN funding. N.R. conducted experiments and contributed to data collection. T.T (corresponding author), supervised the project and contributed to formal analysis, as well as writing—review and editing.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest related to this research.

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