



Original article

Artificial light at night alters urban tree physiology, growth and BVOC emissions depending on tree species

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ABSTRACT

Artificial light at night (ALAN) has been known to affect tree phenology since the mid-20th century, but despite recent studies, the topic remains largely underexplored. The present study aimed to analyse the possible disturbances of ALAN on plant physiology, BVOC emissions and growth in four urban tree species: *Quercus ilex*, *Quercus cerris*, *Liquidambar styraciflua* and *Ginkgo biloba*. The species were selected considering their different botanical families, phenology, and their potential distinct capacities to respond to ALAN. Across the seasons, stem growth, physiological traits (data collected at dawn, midday, and nighttime) and BVOCs were measured in night-illuminated and control trees. The results showed species-specific responses, with higher sensitivity of *G. biloba* in spring. Whereas, in summer, *Q. ilex*, *Q. cerris*, and *L. styraciflua* were more sensitive to ALAN than *G. biloba*, showing reduced P_n and g_s at both dawn and midday, which also affected stem radial growth. Moreover, ALAN significantly increased nocturnal isoprene emissions in *Q. ilex* and *L. styraciflua*, while *G. biloba* showed no response. During autumn, in deciduous species, ALAN preserved leaf photosynthetic functionality (i. e., higher P_n , F_v/F_m , and Chl_{index}) compared to controls, with a parallel delay of leaf senescence except for *G. biloba*. In winter, ALAN altered physiological parameters in *Q. ilex* similarly to summer patterns. These species-specific responses underscore the need to develop species-specific sensitivity tables to ALAN. Such an approach would support informed tree selection and lighting design in urban environments, contributing to the resilience, functionality, and sustainability of urban ecosystems under increasing artificial nighttime illumination.

1. Introduction

Urban environments have rapidly expanded, reshaping landscapes and altering the natural conditions in which plants grow. One of the peculiar characteristics of modern urban ecosystems is the artificial nighttime illumination, predominantly from streetlamps, which might constitute a potential alteration of the natural photoperiodicity that plants have adapted to over evolutionary time scales (Rich and Longcore, 2006). Indeed, light is a fundamental environmental factor for plants, influencing key physiological and biochemical processes including photosynthesis, photomorphogenesis, circadian rhythm regulation, and the synthesis of secondary metabolites (Lauria et al., 2024). Plants have evolved complex photoreceptors, such as phytochromes (mainly for red light), cryptochromes (mainly for blue light),

and phototropins to detect and respond to variations in light intensity, duration, and spectrum. These photoreceptors can modulate growth, development, phenology, and metabolic pathways, helping plants optimise resource allocation under different environmental conditions (Lauria et al., 2024).

The influences of artificial lighting at night (ALAN) on trees have been described since the early 20th century (Matzke, 1936). It was observed that artificial lighting affects tree phenology by altering the timing of critical seasonal events, such as budburst and leaf senescence, delaying the autumnal leaf fall (Chen et al., 2026; Lv et al., 2025), thereby extending the growing season and potentially exposing trees to frost damage or little branch desiccation risks. In recent decades, a more energy-efficient technology, the Light Emitting Diodes (LEDs), was adopted for lighting our cities at night. Although LEDs are more efficient

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and long-lasting than traditional lighting systems (high-pressure sodium lamps), their unique spectral composition, which often includes peaks in the blue and red regions, has raised new concerns regarding their potential impacts on urban tree species (Liu et al., 2021; Lo Piccolo et al., 2024). Recent studies have highlighted that exposure to LED streetlamps can substantially influence tree physiology and morphology. LED streetlamps have been reported to affect tree architecture, stimulating branch elongation and increasing leaf chlorophyll content while concurrently causing leaf physiological alterations (Lauria et al., 2024; Liu et al., 2021; Lo Piccolo et al., 2024). Moreover, artificial night lighting has been linked to the modification of carbon metabolism, evidenced by altered starch and sugar accumulation patterns and downregulation of daytime photosynthesis in several/different species (Kwak et al., 2017; Lo Piccolo et al., 2023). Such observations indicated that trees under ALAN may undergo metabolic alterations, potentially reducing their overall vigour and resilience to environmental stresses (Friulla and Varone, 2025).

Beyond physiological and morphological responses, biogenic volatile organic compounds (BVOCs) represent another important aspect of tree metabolism influenced by environmental conditions (Loreto et al., 1996; Sun et al., 2020). Indeed, BVOC emissions are strongly modulated by temperature, light intensity, and plant physiological status (Bonn et al., 2019; Gil et al., 2013; Loreto and Schnitzler, 2010). BVOCs, such as isoprene and monoterpenes (α -pinene and β -pinene constitute ~50% of the global monoterpene emissions) play crucial roles in atmospheric chemistry, affecting air quality through photochemical reactions that can lead to tropospheric ozone formation (Tripathi and Sahu, 2020). Therefore, it is essential to evaluate whether ALAN can alter the rate or timing of these emissions. Currently, there is no research on whether ALAN induces higher daytime BVOC emissions or whether the intensity of street lighting is sufficient to trigger nocturnal emission events in urban tree species.

Within urban green infrastructure, trees represent pivotal biotic components that mediate key ecosystem services (e.g., thermal regulation, CO₂ sequestration, pollutant filtration, stormwater management, provision of habitats) (Livesley et al., 2016), consequently, elucidating tree physiological responses to ALAN is indispensable for preserving the resilience and functional integrity of urban ecosystems. Moreover, the impact of night LED streetlamps is not uniform across tree species, indicating that species-specific responses must be carefully considered when selecting trees for urban planting projects (Chaney, 2002; Lo Piccolo et al., 2023). Differential sensitivities to light spectra and intensities underscore the importance of targeted research to evaluate the adaptability of urban tree species to lighting conditions.

The present study investigates the impact of LED streetlamp illumination on four selected urban tree species differing in BVOC emissions, physiology, phenology, and taxonomic position. *Ginkgo biloba* L. (Ginkgoaceae), was included as a phylogenetically distinct gymnosperm with isoprene and monoterpenes emissions (Li et al., 2010). *Quercus ilex* L. and *Quercus cerris* L. (Fagaceae) were included to analyse an evergreen and a deciduous species within the same genus; moreover, *Q. ilex* is a high monoterpenes emitter (produced ex novo and not stored) (Niinemets et al. 2002), whereas *Q. cerris* is not a BVOCs emitter (Loreto et al., 1998). *Liquidambar styraciflua* L. (Altingiaceae) was chosen for its high ornamental value and for emitting both isoprene and monoterpenes (tree species with specialised foliar terpene-storing structures) (Nagalingam et al., 2023). We hypothesise that: i) ALAN can alter tree physiology across the diel cycle and also affect BVOCs emission, leading to detectable changes in plant performance compared to non-illuminated controls; ii) the magnitude of ALAN effects varies seasonally, reflecting differences in phenological stage and environmental conditions; iii) tree responses to ALAN are species-specific, resulting in contrasting responses among tree species. Accordingly, analyses of plant morphology, gas exchange, chlorophyll a fluorescence, leaf chlorophyll content, and BVOCs emission, were used to provide new insights into the intricate relationships between urban trees and ALAN.

Improved understanding of these interactions may support urban planners in urban lighting design and tree selection in relation to implementing mitigation strategies aimed at minimising the ecological consequences of ALAN, thereby promoting the resilience and ecological functionality of urban ecosystems.

2. Materials and methods

2.1. Plant material

Twenty saplings of each species (*Q. ilex*, *Q. cerris*, *L. styraciflua* and *G. biloba*) were purchased from a plant nursery (Giorgio Tesi Group Pistoia, Italy). The experiment was conducted from February 2024 to May 2025 in an open experimental field at the Department of Agriculture, Food, Environment and Forestry (43° 48' 57.966" N, 11° 12' 1.788" E). All trees were 3 years old and about 150 cm tall when the experiment started. In February 2024, each tree was transferred to a 30 L container filled with a peat-based substrate. Throughout the trial, the trees were well irrigated and fertilised with slow-release fertiliser (Osmocote® (N: P:K, 15:09:11, 50 g plant⁻¹). Urban-type LED streetlights (model: phLuminaELP2S 4000 K 52 W; Phaenomena, Montesano sulla Marcellana (SA), Italy) were installed roughly 40 cm above the canopy (for all analyses, leaves located in the portion of the canopy approximately 40 cm from the light source were used). Beginning in May 2024, half of the individuals of each species (10 trees) were exposed to ALAN treatment (Trt) delivering approximately 130 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of photosynthetically active radiation (PAR) at canopy level (Fig. S1); an astronomical timer switched the lamps on and off to mimic typical city lighting schedules. The positions of the trees relative to the lamps were randomly assigned. The remaining 10 trees per species were not night-illuminated and analysed as controls (Cnt; no PAR was detected at night). Physiological (gas exchange and chlorophyll a fluorescence analyses) and dual-ex measurements were taken on fully expanded leaves in July 2024 (summer), on senescing leaves during autumn–winter 2024 (October for *L. styraciflua*, November for *Q. cerris*, and *G. biloba*, January for *Q. ilex* [were measured leaves of the past year]), and on newly emerged leaves in May 2025 (spring) at four moments in the diel cycle: dawn (1 h after sunrise), solar noon, and at the beginning of the night (2 h after sunset). Mean monthly temperatures, precipitation and solar radiation of the entire experimental period are reported in Fig. S2.

2.2. Gas exchange analyses

Leaf gas exchange parameters were measured on six independent trees ($n = 6$) with a portable infrared gas analyser the LI-6800 system (Li-Cor, Lincoln, NE, USA). Measurements were recorded from randomly selected leaves (at a distance of ~40–50 cm from the streetlamp) 1 h after sunrise (sunrise), at zenith and 2 h after sunset, at the beginning of the night (night), according to the monthly sun path. For daylight measurements, a 6800–01 A LED light source with a light intensity of 400–1800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was used, according to the external ambient PAR. For night measurements, a 6800–12 A clear-top chamber was used, with the ambient light as the light source. Inside the leaf chamber, the CO₂ concentration was set to 400 $\mu\text{mol mol}^{-1}$ using the CO₂ mixer, the leaf temperature was at ~25 °C (spring–autumn), ~30 °C (summer) and ~15 °C (winter time), the relative humidity was maintained at ~50%, and the flow rate was 600 $\mu\text{mol s}^{-1}$. Once the steady state was reached, the net CO₂ assimilation rate (P_n), stomatal conductance (g_s), and intercellular CO₂ concentration (C_i) were determined.

2.3. Chlorophyll a fluorescence analysis

Chlorophyll a fluorescence was detected using a Plant Efficiency Analyser fluorimeter (Handy-PEA; Hansatech Ltd., Norfolk, UK). The same leaves used for gas-exchange measurements or the nearest ($n = 6$) were examined at each sampling date and time. Leaves were dark-

adapted for 20 min in 4 mm leaf clips, after a 1 s saturating red flash light ($\approx 3000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) was performed and elicited fluorescence was recorded. The maximal photochemical efficiency of photosystem II (PSII) was expressed as F_v/F_m , where $F_v = (F_m - F_0)$; F_0 represents the initial fluorescence extrapolated from the first microseconds of illumination, and F_m is the fluorescence peak reached during the saturating pulse. Moreover, OJIP transients were analysed. From the JIP-test (Strasser et al., 2004), derived flux variables (i.e., quantum yield for electron transport at $t = 0$ [Φ_{E0}], quantum yield for the reduction of end acceptors of PSI [Φ_{R0}], and dissipated energy flux per cross section [DI_0/CS_0]) were analysed.

2.4. Chlorophyll index analyses

An Optical Leafclip Meter DUALEX (METOS®, Weiz, Austria) was used to measure chlorophyll index ($\text{Chl}_{\text{index}}$). Similar leaves, used for physiological measurements, were analysed at each sampling date and time. The analyses of $\text{Chl}_{\text{index}}$ were carried out on 30 leaves for each species and treatment.

2.5. BVOC sampling and analyses

Isoprene and α -pinene emissions were measured in real-time ($n = 3$ leaves from three independent trees per treatment) concurrently with leaf gas exchange (summer and autumnal/winter analyses) by connecting the LI-6800 leaf chamber to glass thermal desorption (TD) sampling traps (GERSTEL GmbH & Co. KG) via a Teflon connection. BVOCs were collected by actively drawing air from the leaf chamber through the TD traps using a BUCK Elite™ (model Elite-1) Personal Air Sampler. The TD traps were packed with a combination of activated graphitised black carbon adsorbents supplied by Lara Laboratori (Formello, Rome, Italy): Carbograph® 1 (20/40 mesh, surface area $100 \text{ m}^2 \text{g}^{-1}$, weak sorption strength, hydrophobic), and Carbograph® 2S (20/40 mesh, surface area $13 \text{ m}^2 \text{g}^{-1}$ medium sorption strength, hydrophobic). Adsorbents were arranged within glass tubes in order of increasing sorption strength following the airflow direction, with Carbograph® 2S positioned upstream of Carbograph® 1. Unsilanised quartz wool (Machery-Nagel GmbH & Co. KG) plugs were inserted between the adsorbents layers to separate and keep them inside the trap. Before the first use, TD traps were conditioned by thermal cleaning under a nitrogen flow of 100 mL min^{-1} , first at 300°C for 15 min and subsequently at 310°C for 10 min with a ramp of 5°C min^{-1} . After conditioning, traps were immediately sealed with Swagelok® end caps fitted with PTFE ferrules and stored until use. Following sampling, TD traps were kept at 4°C and analysed within one week. For each tree species, BVOCs were collected by sampling a total air volume of 2 L at a constant flow rate of 200 standard cubic centimetres per minute (scm). Background air samples were obtained from the empty cuvette both before and after the leaf measurement and were subtracted from the corresponding leaf-enclosed samples to correct emission values. Quantification was achieved using external calibration curves prepared from authentic reference standards of isoprene (>99%) and α -pinene (>98%) purchased from Sigma-Aldrich. Standard curves were prepared in Tedlar® bags with PTFE fittings and serially diluted with nitrogen to obtain an eleven- and seven-points calibration curves for isoprene and α -pinene, respectively. For each calibration level, a single TD trap was sampled using the same flow rate and sampling duration applied for plant measurements. Blank samples were obtained by sampling Tedlar® bags filled with nitrogen only.

TD traps were desorbed using a gas-chromatograph 8890 GC System (Agilent Technologies) coupled with an MSD mass detector 5977 C (Agilent Technologies) and a thermal-desorber TDU 2 (GERSTEL). Primary desorption was conducted at 300°C for 5 min with a desorption flow of 50 mL min^{-1} , during which analytes were transferred to a cryofocusing trap containing 15 mg of Tenax® TA maintained at -20°C , applying a septum purge flow of 4 mL min^{-1} . Following primary

desorption, the cold trap was rapidly heated to 300°C and held for 19 min to inject analytes into the GC system. Chromatographic separation was performed using an DB-WAX Ultra Inert capillary column (60 m, $250 \mu\text{m}$ diameter, $0.5 \mu\text{m}$ film thickness, Agilent Technologies). Helium was used as the carrier gas at a constant flow rate of 1.2 mL min^{-1} . The oven temperature program consisted of an initial hold at 40°C for 1 min, followed by a ramp of 5°C min^{-1} to 230°C and a second ramp of $30^\circ\text{C min}^{-1}$ to a final hold at 250°C for 4 min. Analytes were ionised at 70 eV in the ion source at 230°C and detected both in full scan (29–300 amu) and single ion monitoring (SIM) with ions m/z 52, 67, and 68 for isoprene and ions m/z 93, 121 and 136 for α -pinene. Raw data were acquired with an Agilent ChemStation and quantified by MassHunter Workstation Quantitative Analysis (v. 12, Agilent Technologies). BVOCs emission fluxes were calculated and expressed in $\text{nmol m}^{-2} \text{s}^{-1}$. *Quercus cerris* was not further analysed since it was a very low emitter (i.e., very low emissions in summer; Fig. S4), and as confirmed by negligible emissions observed by Loreto et al. (1998).

2.6. Tree annual radial stem growth

Throughout the entire experiment, three randomly chosen trees from each species and treatment were fitted with point dendrometers positioned at mid-stem height. These automatic sensors recorded stem radius variations every 15 min. Stem radius variations measured by dendrometers monitor the reversible changes of stem radius, referring to daily water status (shrinkage and swelling phases), and the irreversible changes of wood formation (Deslauriers et al., 2007). The dendrometer measured the linear displacement of a sensing rod pressed against the bark (DENDROLOG Rossi Strumenti SRLS—Scandicci, Italy) by recording stem radius variation from 0 to 12 mm with an average sensitivity of 0.3 mm. The movement was converted to a 0–10 V signal by a transducer (FL SENS 3.3 V, Rossi Strumenti SRLS) and digitised via an analogue-to-digital converter (datalogger FL SENS) linked to a computer for continuous storage. The stem diameter series were shown as stem diameter variation (μm) to study trends and patterns within treated plants. In detail, dendrometer time series were obtained by subtracting the initial value to each measurement of specific tree per treatment.

2.7. Statistical analyses

The normality of the data was assessed using the Shapiro-Wilk test, and the homoscedasticity was examined using the Brown-Forsythe test. Plant physiological (gas-exchange and chlorophyll a fluorescence) and $\text{Chl}_{\text{index}}$ were compared by two-way ANOVA with treatment and time of the day as the source of variation for each species. All the means were separated by Fisher's least significant difference (LSD) post-hoc test ($P < 0.05$). When the F ratio of the interaction between the variability factors was not significant, for each treatment, the means were subjected to one-way ANOVA with time as the source of variation; in case of non-homoscedastic data, a Welch ANOVA and Dunnett's T3 multiple comparison test were performed. Capital and Greek letters indicate statistically significant differences over time for controls and treated, respectively. For each timepoint, means were subjected to Student's *t*-test, and differences between treatments were indicated by asterisks ($P < 0.05$: *; $P < 0.01$: **; $P < 0.001$: ***); in case of non-homoscedastic data, a Welch *t*-test was performed. Isoprene and α -pinene emission data were analysed, for each timepoint and treatment, by Student's *t*-test. The software used for the statistical analyses was GraphPad 10 (GraphPad, La Jolla, CA, USA). The normalised stem diameter time series were interpolated by fitting Gompertz functions (Giovannelli et al., 2007) by using OriginPro v8.0 (OriginLab, Northampton, MA, USA). The Gompertz functions, nonlinear regressions, estimate the pattern of intra-annual secondary growth (*y*) against time (*t*, in DOY):

$$(y = a \cdot e^{(-k(x-c))}),$$

where the parameters a , k and c are the growth asymptotes, time axis placement, and rate of change of the curve, respectively.

3. Results

3.1. Gas exchange analyses

In spring, at night, leaves of all four tree species analysed showed higher and positive P_n and lower C_i values in Trt than Cnt (Cnt; Fig. 1a,b,c,d,i,j,k,l).

In *Q. ilex* trees, no differences in P_n values were observed at dawn and midday between treatments, yet g_s values were lower in Trt than Cnt at dawn, while C_i values were lower in Trt only at midday (Fig. 1a,e,i). At dawn *Q. cerris* did not show differences in P_n and g_s values between treatments, while at midday, Trt trees showed higher P_n and g_s values than Cnt trees (Fig. 1b,f). In *L. styraciflua* trees, at dawn, g_s values were higher in Trt than Cnt, but no differences in P_n were observed, while at midday, Cnt trees showed higher P_n followed by higher g_s values than Trt (Fig. 1c,g). *G. biloba* trees showed lower P_n and g_s values in Trt than Cnt at both dawn and midday (Fig. 1d,h).

In summer, as in spring, leaves of all four tree species analysed showed higher and positive P_n and lower C_i values in Trt than in Cnt, at night (Fig. 2a,b,c,d,i,j,k,l). Moreover, at night, only *L. styraciflua* and *G. biloba* showed higher g_s values in Trt than in Cnt (Fig. 2g,h).

At both dawn and midday, *Q. ilex*, *Q. cerris* and *L. styraciflua* Trt trees showed lower P_n and g_s values than relative Cnt, while *G. biloba* showed no differences between treatments (Fig. 2a,b,c,d,e,f,g,h).

In autumn, at night, leaves of *Q. cerris* and *L. styraciflua* Trt trees showed higher and positive P_n values and lower C_i values than Cnt trees, except for *G. biloba* trees, which showed negative but higher P_n values than Cnt, also showing no statistical differences in C_i values between

treatments (Fig. 3b,c,d,j,k,l). At night, during winter, *Q. ilex* showed no statistical differences in night P_n values between treatments, despite Trt trees exhibited positive P_n values and lower C_i values compared to Cnt (Fig. 3a,i).

In autumn, *Q. cerris* Trt trees showed higher P_n values than Cnt at both dawn and midday, while *L. styraciflua* Trt trees only at midday, also showing higher g_s values than relative Cnt (Fig. 3b,c,g). The difference between treatments in *G. biloba* trees was observed at midday, with higher values in P_n obtained in Trt than Cnt trees (Fig. 3d). In winter, *Q. ilex* showed lower P_n and g_s values in Trt trees than Cnt trees at dawn, while no statistical differences were observed at midday (Fig. 3a,e).

3.2. Chlorophyll a fluorescence analysis

In spring, leaves of *Q. ilex* trees showed no differences in F_v/F_m , Φ_{E0} , Φ_{R0} , and DI_0/CS_0 between treatments (Fig. 4a,e,i,m). For *Q. cerris* trees, lower F_v/F_m and Φ_{E0} values were observed at midday in Cnt than Trt trees; whereas higher Φ_{E0} , Φ_{R0} values were observed at night in Trt than Cnt trees (Fig. 4b,f,j). In *L. styraciflua* trees the Φ_{R0} parameter was different between treatments, with lower values in Trt than Cnt trees observed at both dawn and night (Fig. 4k). *G. biloba* trees reported the highest differences between treatments, showing at both dawn, midday and night, lower values in F_v/F_m , Φ_{E0} , Φ_{R0} and higher in DI_0/CS_0 in Trt compared to Cnt (Fig. 4d,h,l,p).

In summer, no differences between treatments were observed for F_v/F_m , Φ_{E0} , and DI_0/CS_0 parameters in leaves of all four tree species (Fig. 5a,b,c,d,e,f,g,h,m,n,o,p).

Treated trees of *Q. ilex*, *Q. cerris* and *L. styraciflua* showed lower Φ_{R0} values at both dawn and midday than Cnt, and for *L. styraciflua* also at night (Fig. 5i,j,k). *G. biloba* showed a similar trend only at dawn and night (Fig. 5l).

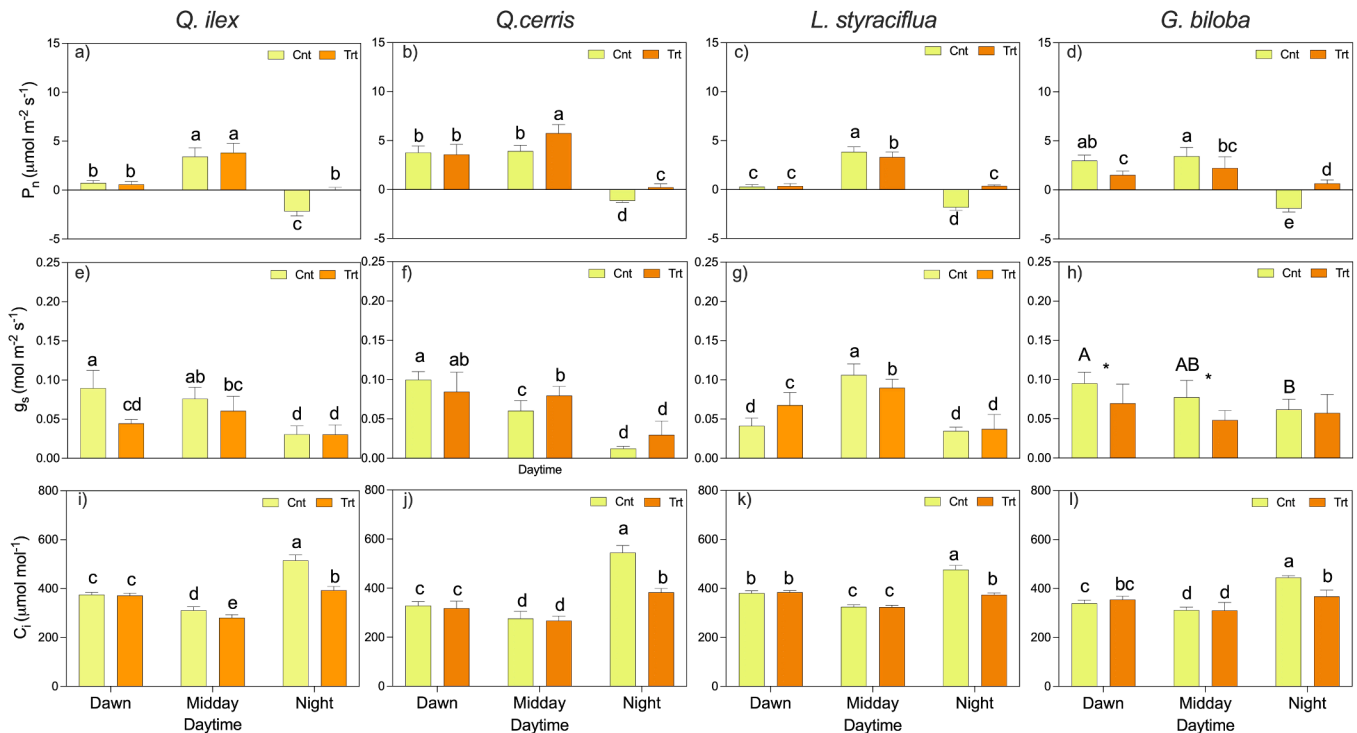


Fig. 1. Spring net CO_2 assimilation (P_n ; a,b,c,d), stomatal conductance (g_s ; e,f,g,h) and intercellular CO_2 concentration (C_i ; i,j,k,l), in *Q. ilex*, *Q. cerris*, *L. styraciflua* and *G. biloba* trees, respectively. The parameters ($n = 6$) were measured at dawn, midday and night in young leaves of controls (Cnt; green bars) and trees grown under ALAN (Trt; orange bars). Means $\pm$ SD were subjected to two-way ANOVA with treatment and timepoint as the source of variation. Means with different letters are significantly different after Fisher's LSD post-hoc test ($P \leq 0.05$). When the F ratio of the interaction between the variability factors was not significant, for each treatment, the means were subjected to one-way ANOVA with time as the source of variation. Capital letters indicate statistically significant differences over time for controls and treated, respectively. For each timepoint, means were subjected to Student's t -test, and differences between treatments were indicated by asterisks ($P < 0.05$: *; $P < 0.01$: **; $P < 0.001$: ***).

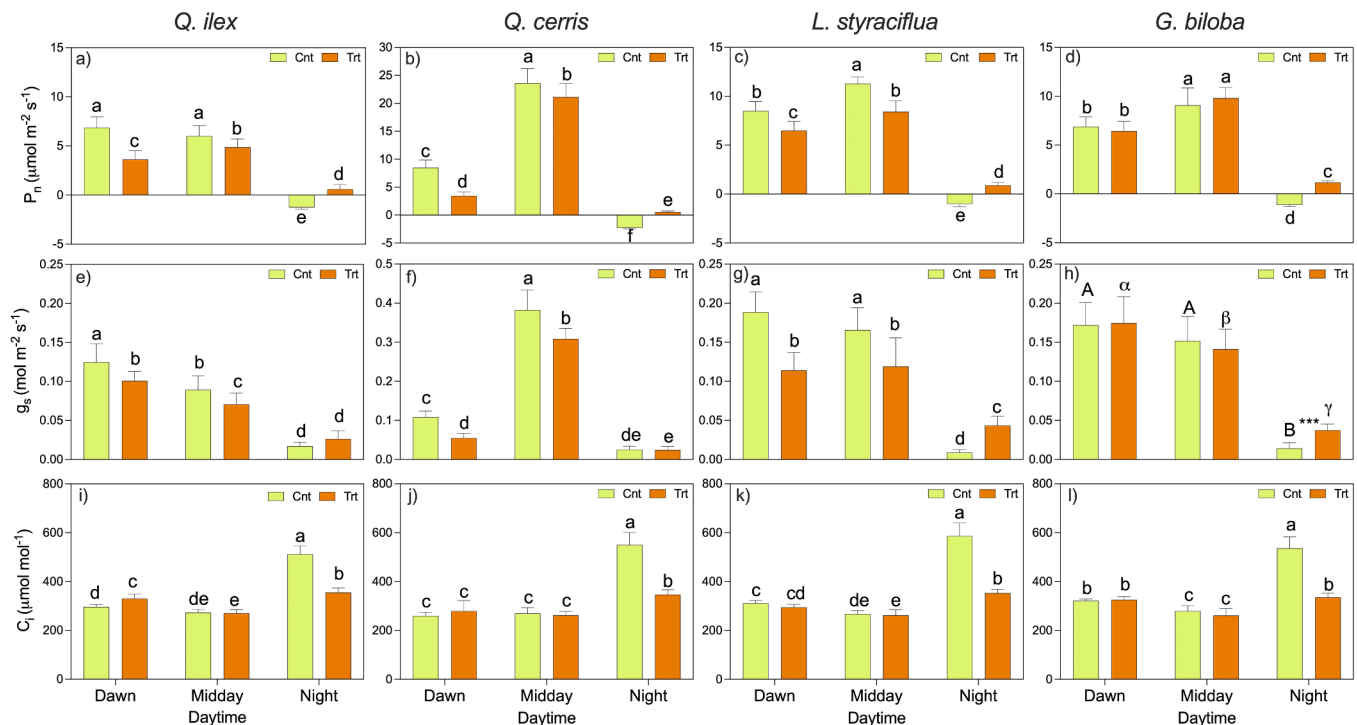


Fig. 2. Summer net CO₂ assimilation (P_n ; a,b,c,d), stomatal conductance (g_s ; e,f,g,h) and intercellular CO₂ concentration (C_i ; i,j,k,l), in *Q. ilex*, *Q. cerris*, *L. styraciflua* and *G. biloba* trees, respectively. The parameters ($n = 6$) were measured at dawn, midday and night in mature leaves of controls (Cnt; green bars) and trees grown under ALAN (Trt, orange bars). Means $\pm$ SD were subjected to two-way ANOVA with treatment and timepoint as the source of variation. Means with different letters are significantly different after Fisher's LSD post-hoc test ($P \leq 0.05$). When the F ratio of the interaction between the variability factors was not significant, for each treatment, the means were subjected to one-way ANOVA with time as the source of variation. Capital and Greek letters indicate statistically significant differences over time for controls and treated, respectively. For each timepoint, means were subjected to Student's *t*-test, and differences between treatments were indicated by asterisks ($P < 0.05$: *, $P < 0.01$: **, $P < 0.001$: ***).

In winter, at night, leaves of *Q. ilex* trees showed lower values in the F_v/F_m parameter, followed by higher Φ_{E0} and DI_0/CS_0 values in Trt than Cnt trees (Fig. 6a,e,m).

In autumn, *Q. cerris* showed higher F_v/F_m , Φ_{E0} and Φ_{R0} values in Trt than Cnt trees, and also lower DI_0/CS_0 values in Trt than Cnt trees at each timepoint (Fig. 6b,f,j,n). In *L. styraciflua*, Trt trees showed higher F_v/F_m values at midday and night than Cnt trees (Fig. 6c), followed by higher DI_0/CS_0 values in Cnt trees (Fig. 6o). Regarding *G. biloba*, Trt trees at midday showed higher values in F_v/F_m , Φ_{E0} and Φ_{R0} parameters and lower values in DI_0/CS_0 than Cnt trees (Fig. 6d,h,l,p).

3.3. Chlorophyll index analyses

In spring, leaves of *Q. ilex* and *Q. cerris* trees showed higher Chl_{index} in Trt than Cnt trees at each timepoint analysed (Fig. 7a,b), while no or very weak statistical differences between treatments were observed in *L. styraciflua* and *G. biloba* trees (Fig. 7c,d).

In summer, *Q. ilex* trees showed higher Chl_{index} in Cnt than Trt trees at dawn and night (Fig. 7e), while again *Q. cerris* showed a similar spring trend (Fig. 7e,f). In both *L. styraciflua* and *G. biloba* trees Chl_{index} values were higher in Cnt than Trt trees only at midday (Fig. 7g,h).

In winter, the only difference in *Q. ilex* trees was observed at midday, showing higher Chl_{index} values in Trt than Cnt trees (Fig. 7i).

In autumn, *Q. cerris* and *G. biloba* showed higher Chl_{index} values in Trt than Cnt trees at each timepoint analysed (Fig. 7j,l), while *L. styraciflua* showed higher Chl_{index} values in Trt than Cnt at both dawn and night (Fig. 7k).

3.4. BVOCs sampling and analyses

In summer, no significant differences in isoprene emissions were

detected at midday in *Q. ilex* between Trt and Cnt trees. However, at night, Cnt trees reduced isoprene emissions by 73.6% compared to midday values, whereas Trt trees exhibited emission levels comparable to those measured at midday, resulting in higher nocturnal isoprene emissions compared to Cnt (Fig. 8a). Regarding α -pinene emissions, no differences between Cnt and Trt trees at midday were detected. Whereas at night, α -pinene emissions increased by 90.3% in Cnt compared to those observed at midday, while Trt trees exhibited values similar to midday levels (Fig. 8b). In winter, no isoprene emissions were detected in *Q. ilex*, while α -pinene showed only very low nocturnal emissions in both treatments, with no significant differences (Fig. 8c,d).

In summer, *L. styraciflua* showed no differences in midday isoprene emissions between Cnt and Trt trees. At night, isoprene emissions were not detectable in Cnt trees, whereas Trt trees reduced emissions by 47.6% compared to midday values (Fig. 8e). The α -pinene emissions exhibited a similar but opposite pattern with nocturnal emissions not detectable in Trt trees, while Cnt trees displayed values comparable to those measured at midday (Fig. 8f). In autumn, isoprene emissions at midday were higher in Trt trees than in Cnt by 140.8%, while no detectable emissions were observed at night (Fig. 8g). The α -pinene was detected only in Trt trees at midday (Fig. 8h).

In summer, in *G. biloba*, no differences in midday isoprene emissions were detected between Cnt and Trt trees, and no detectable emissions were observed at night (Fig. 8i). A similar pattern was also observed for α -pinene (Fig. 8j). In autumn, only Trt trees showed detectable isoprene and α -pinene emissions at midday (Fig. 8k,l).

3.5. Tree annual radial stem growth

The stem diameter series presented different trends reaching diverse levels of diameter growth among treatments (different growth

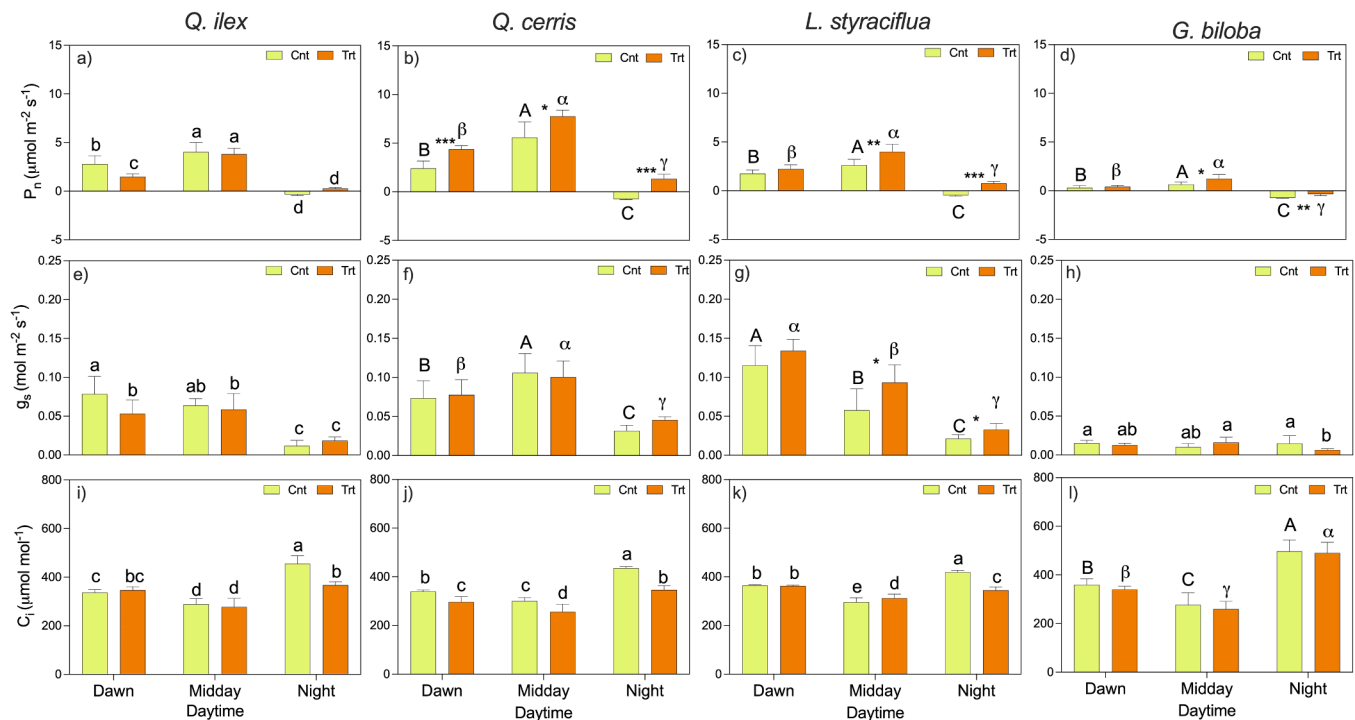


Fig. 3. Winter and autumnal net CO₂ assimilation (P_n ; a,b,c,d), stomatal conductance (g_s ; e,f,g,h) and intercellular CO₂ concentration (C_i ; i,j,k,l), in *Q. ilex*, *Q. cerris*, *L. styraciflua* and *G. biloba* trees, respectively. The parameters ($n = 6$) were measured at dawn, midday and night in senescing leaves (in *Q. ilex* were measured leaves of the past year) of controls (Cnt; green bars) and trees grown under ALAN (Trt, orange bars). Means $\pm$ SD were subjected to two-way ANOVA with treatment and timepoint as the source of variation. Means with different letters are significantly different after Fisher's LSD post-hoc test ($P \leq 0.05$). When the F ratio of the interaction between the variability factors was not significant, for each treatment, the means were subjected to one-way ANOVA with time as the source of variation. Capital and Greek letters indicate statistically significant differences over time for controls and treated, respectively. For each timepoint, means were subjected to Student's *t*-test, and differences between treatments were indicated by asterisks ($P < 0.05$: *; $P < 0.01$: **; $P < 0.001$: ***) in case of non-homoscedastic data, a Welch *t*-test was performed.

asymptotes of Gompertz function with higher values in Cnt than Trt conditions) in *Q. ilex*, *Q. cerris* and *L. styraciflua* (Fig. 9,a,b,c). Whereas the stem diameter series of *G. biloba* reached the same diameter growth in Cnt and Trt trees (e.g., reaching a values of Gompertz function 2911 and 2933 μm in Cnt and Trt, respectively) (Fig. 9d). Moreover, c values showed the highest rate of change of the curve in Cnt of *Q. cerris* and *L. styraciflua*, and in Trt of *Q. ilex*.

4. Discussion

This study provides novel insights into the influence of ALAN on tree physiological responses. Our results revealed seasonal divergence in daytime responses of analysed trees, indicating that ALAN impact is highly dependent on the leaf developmental stage and species. These findings align with the accumulating evidence that ALAN represents an emerging abiotic stressor capable of affecting plant physiological processes through multiple, interacting pathways (Friulla and Varone, 2025; Kwak et al., 2018).

4.1. ALAN induced different species-specific physiological responses across the leaf developmental stages

Across all seasons and species, a consistent pattern emerged during nighttime measurements, with leaves exposed to ALAN displaying positive P_n and reduced C_i compared to controls. This finding supports previous evidence that even low-intensity nocturnal light, irrespective of whether the streetlamp source is old high-pressure sodium (HPS) or new LED technology, may stimulate nocturnal CO₂ fixation (Kwak et al., 2018; Lo Piccolo et al., 2024). Nocturnal illumination may partly mimic continuous light exposure, extending photosynthetic activity into the dark period and, over time, altering the natural photoperiod. Such

alterations can interfere with circadian regulation and cause functional disorders in the photosynthetic apparatus (Lo Piccolo et al., 2023; Velez-Ramirez et al., 2011; Zha et al., 2019). Further studies are needed to identify species-specific thresholds of light intensity and spectral composition below which nocturnal photosynthetic stimulation and associated physiological alterations are minimised, thereby providing a basis for developing lighting strategies that reduce the ecological and physiological impacts of ALAN.

4.1.1. Spring responses

Overall, in spring, young expanding leaves of *Q. ilex*, *Q. cerris*, and *L. styraciflua* exposed to ALAN showed few differences in physiological responses compared to respective controls. In *Q. ilex* and *L. styraciflua* species, dawn measurements revealed a decoupling between stomatal behaviour and photosynthetic activity characterised by very low CO₂ assimilation rates, indicating a predominant regulating role of non-stomatal factors (e.g., biochemical constraints) on leaf photosynthesis. On the other hand, at midday, all three species analysed show a more stomatal control of photosynthesis. In *Q. cerris*, the elevated P_n values observed at midday in ALAN-treated trees were associated with increased g_s , higher F_v/F_m , and Φ_{E0} values compared to control trees. This response suggests better preservation of PSII functionality and reduced photoinhibition under high light conditions, such as those occurring at midday (Lichtenthaler and Burkart, 1999; Yu et al., 2020). To our best knowledge, only one work has examined physiological data also on young, expanding leaves in *Platanus x acerifolia* and *Tilia platyphyllos* trees subjected to ALAN, reporting lower sensitiveness to night-illumination compared to mature and senescent ones, supporting our results on *Q. ilex*, *Q. cerris*, and *L. styraciflua* (Lo Piccolo et al., 2023). The limited sensitivity of young leaves in these species could be explained since young, expanding leaves generally have limited

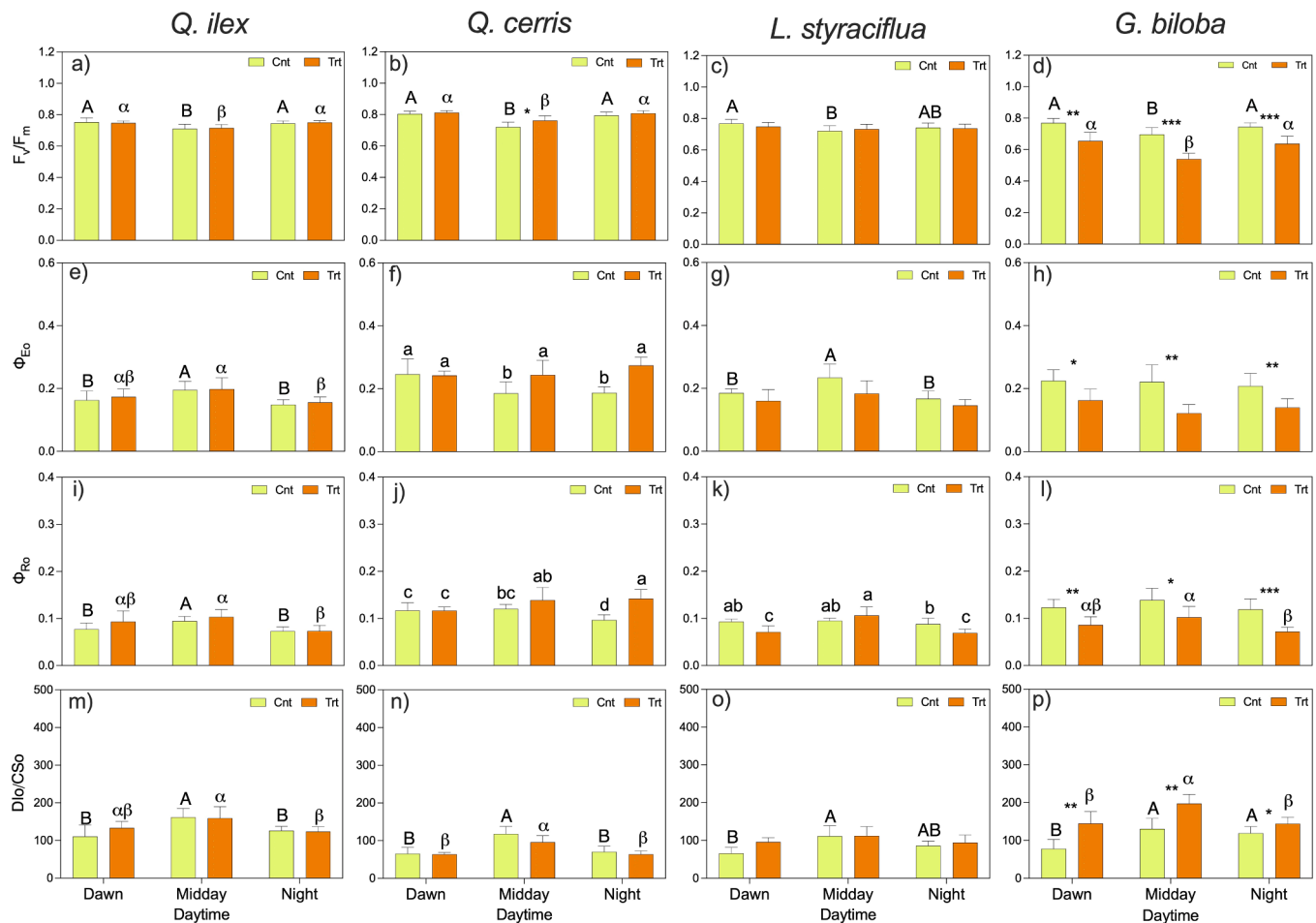


Fig. 4. Spring PSII maximum quantum yield (F_v/F_m ; a,b,c,d), quantum yield for electron transport at $t = 0$ (Φ_{Eo} e,f,g,h), quantum yield for the reduction of end acceptors of PSI (Φ_{Ro} ; i,j,k,l), and dissipated energy flux per cross section (DI_o/CS_o ; m,n,o,p), in *Q. ilex*, *Q. cerris*, *L. styraciflua* and *G. biloba* trees, respectively. The parameters ($n = 6$) were measured at dawn, midday and night in young leaves of controls (Cnt; green bars) and trees grown under ALAN (Trt, orange bars). Means $\pm$ SD were subjected to a two-way ANOVA with treatment and timepoint as the source of variation. Means with different letters are significantly different after Fisher's LSD post-hoc test ($P \leq 0.05$). When the F ratio of the interaction between the variability factors was not significant, for each treatment, the means were subjected to one-way ANOVA with time as the source of variation; in case of non-homoscedastic data, a Welch ANOVA and Dunnett's T3 multiple comparison test were performed. Capital and Greek letters indicate statistically significant differences over time for controls and treated, respectively. For each timepoint, means were subjected to Student's t -test, and differences between treatments were indicated by asterisks ($P < 0.05$: *; $P < 0.01$: **; $P < 0.001$: ***).

photosynthetic capacity and chlorophyll content compared to mature ones (see Fig. S3), as the photosynthetic apparatus (e.g., photosystems and antenna complexes) is still not fully assembled (Bertamini, 2003; Niinemets, 2016b). Consequently, young leaves may be less responsive to ALAN influence. In contrast, young *G. biloba* leaves of trees grown under ALAN treatment exhibited pronounced daylight reductions in photosynthetic rates, due to both stomatal (i.e., reduced g_s values) and non-stomatal limitations (i.e., reduced F_v/F_m , Φ_{Eo} and Φ_{Ro} values) compared to the controls. Stomatal response represents the first and rapid defence response allowing plants to quickly adjust to environmental changes by modulating leaf gas exchange with consequent reduction in CO_2 fixation (Kollist et al., 2019). A reduction in photosynthetic activity causes plants to absorb more light energy than can be effectively used for CO_2 fixation. Indeed, it should be noted that the increase in the leaf Chl_{index} between young and mature leaves in *G. biloba* was smaller than in the other species, suggesting contents more similar to those of mature leaves (Fig. S3). This surplus energy may lead to elevated production of reactive oxygen species (ROS), which have been shown to interfere with the synthesis of the PSII core protein D1, thus delaying the PSII repair and consequently limiting the entire photosynthetic electron transport chain (that is not fully developed in young leaves) (Bertamini and Nedunchezian, 2002; Takahashi and

Murata, 2008). Consistent with this interpretation, Kwak et al. (2018) in a study conducted on *Liriodendron tulipifera* trees grown under ALAN (HPS-lamp), reported that the reduced photochemical efficiency observed in leaves was due to photodamaged PSII. Therefore, in spring, we suggest that the observed decline in F_v/F_m in ALAN-treated *G. biloba* young expanding leaves with a parallel increase in energy dissipated per leaf cross-section (DI_o/CS_o) and consequent reduction in the quantum yield for the reduction of end acceptors of PSI is due to an imbalance between PSII photodamage and repair of photodamaged PSII (Kwak et al., 2018; Takahashi and Badger, 2011). Overall, this highlights that young leaves of *G. biloba* are more susceptible to ALAN than those of the other tree species analysed. The latter, by accumulating chlorophyll more gradually during leaf development, may have maintained a tighter coordination between pigment content and electron transport capacity, which could explain their fewer variable responses. However, this effect appears to be transient, as mature *G. biloba* leaves showed no significant differences between treatments, while only weak differences were observed at the senescent stage, suggesting a capacity for acclimation or reduced sensitivity to ALAN at later developmental stages.

4.1.2. Summer responses

During summer, a more generalised impact of ALAN on mature

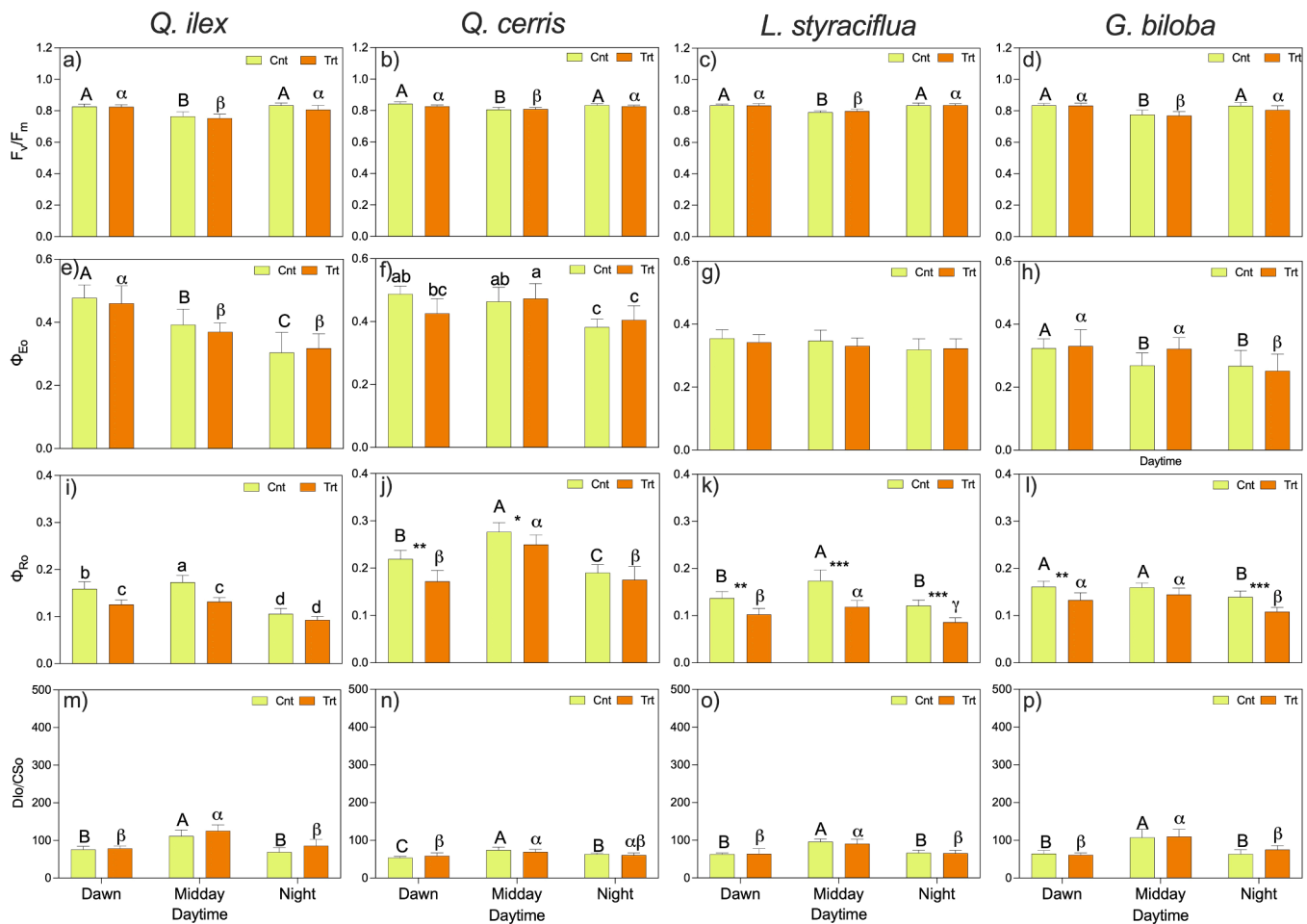


Fig. 5. Summer PSII maximum quantum yield (F_v/F_m ; a,b,c,d), quantum yield for electron transport at $t = 0$ (Φ_{E0} e,f,g,h), quantum yield for the reduction of end acceptors of PSI (Φ_{R0} ; i,j,k,l), and dissipated energy flux per cross section (DI_0/CS_0 ; m,n,o,p), in *Q. ilex*, *Q. cerris*, *L. styraciflua* and *G. biloba* trees, respectively. The parameters ($n = 6$) were measured at dawn, midday and night in mature leaves of controls (Cnt; green bars) and trees grown under ALAN (Trt, orange bars). Means $\pm$ SD were subjected to a two-way ANOVA with treatment and timepoint as the source of variation. Means with different letters are significantly different after Fisher's LSD post-hoc test ($P \leq 0.05$). Capital and Greek letters indicate statistically significant differences over time for controls and treated, respectively. For each timepoint, means were subjected to Student's t -test, and differences between treatments were indicated by asterisks ($P < 0.05$: *, $P < 0.01$: **, $P < 0.001$: ***).

leaves was observed at both dawn and midday in *Q. ilex*, *Q. cerris*, and *L. styraciflua*, with reduced P_n accompanied by a parallel decline in g_s values compared to controls. A similar trend has been reported in previous studies conducted on ALAN-treated *Populus alba* (Lo Piccolo et al., 2024), *L. tulipifera* (Kwak et al., 2017), *Euonymus japonicus* and *Rosa hybrida* (Wei et al., 2023). These effects have been attributed to dysfunctional stomatal movement and reduced guard cell turgor linked to alterations in leaf starch and ABA metabolism (Kwak et al., 2017; Lo Piccolo et al., 2024). *G. biloba*, a deciduous gymnosperm often regarded as a living fossil, is known for its tolerance against common urban environmental stresses (Zhao et al., 2019). The absence of stomatal alterations in *G. biloba* mature leaves, together with similar P_n values at dawn and midday between treatments, suggests a reduced sensitivity to ALAN in this relict species. Whether gymnosperms are generally less responsive to ALAN than angiosperms remains an open question and warrants targeted investigation.

In mature leaves, despite the reductions in net CO_2 assimilation observed in *Q. ilex*, *Q. cerris*, and *L. styraciflua*, key indicators of leaf photochemistry, such as F_v/F_m and Φ_{E0} , were not significantly affected by the ALAN treatment, indicating the absence of PSII photodamage, likely due to the effective photoprotective capacity of mature leaves. However, we observed that the quantum yields of reactions after Q_B were susceptible to ALAN, impacting the efficiency of the electron flow reaching the acceptor side of PSI. A reduction in Φ_{R0} reflects limited

electron flow to terminal PSI acceptors, such as $NADP^+$, and is consistent with a downstream constraint potentially linked to reduced metabolic sink capacity in leaves exposed to ALAN (i.e., slowdown of Calvin cycle due to stomatal limitations) (Kumar et al., 2022; Lo Piccolo et al., 2024). Under such conditions, electrons may accumulate without being effectively utilised, leading to potential NADPH accumulation and a depletion of oxidised $NADP^+$, thereby limiting the availability of terminal electron acceptors at PSI (Chaux et al., 2015; Czaja and Kolton, 2026; Li et al., 2021).

Despite the absence of differences in gas exchange parameters, *G. biloba* trees exposed to ALAN exhibited a consistent reduction in Φ_{R0} compared to Cnt trees at both dawn and night. We suggest that, under ALAN, the nighttime rate of photochemical electron generation exceeds the metabolic sink capacity (i.e., very low P_n). This imbalance may persist into the early photoperiod, potentially affecting other tree species as well, and could explain the observed reduction in Φ_{R0} at dawn. Overall, the consistent response across species of Φ_{R0} could make this parameter a promising indicator for detecting ALAN-induced physiological disturbances, supporting more informed decisions in urban tree management.

Leaf chlorophyll index (Chl_{index}) responses further emphasised the strong species specificity of ALAN effects. For example, in summer, Chl_{index} was high at dawn and at night in control trees of *Q. ilex*, and at midday in control trees of both *L. styraciflua* and *G. biloba*, whereas in

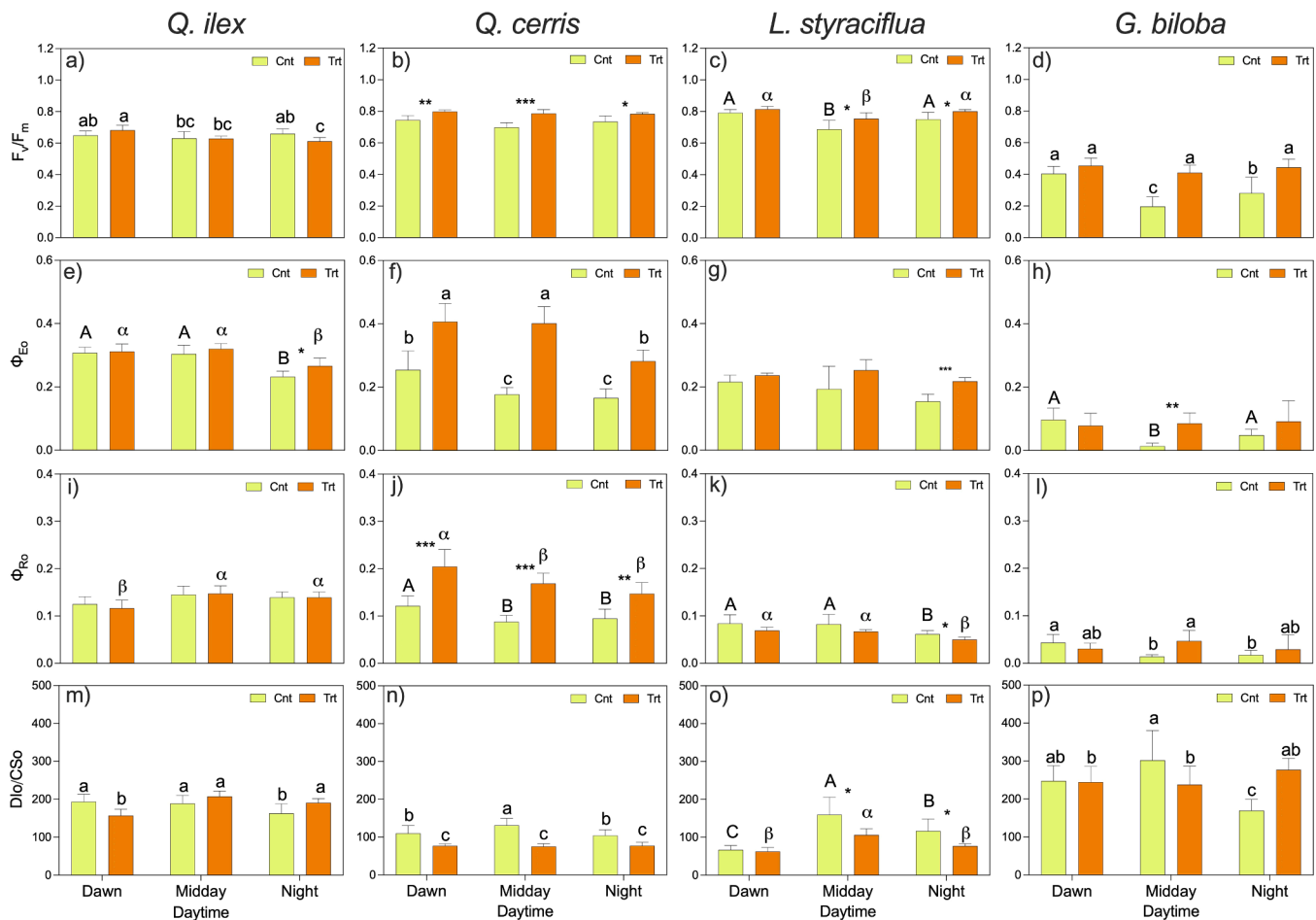


Fig. 6. Winter and autumn PSII maximum quantum yield (F_v/F_m ; a,b,c,d), quantum yield for electron transport at $t = 0$ (Φ_{E0} e,f,g,h), quantum yield for the reduction of end acceptors of PSI (Φ_{Ro} ; i,j,k,l), and dissipated energy flux per cross section (DI_0/CS_0 ; m,n,o,p), in *Q. ilex*, *Q. cerris*, *L. styraciflua* and *G. biloba* trees, respectively. The parameters ($n = 6$) were measured at dawn, midday and night in senescing leaves (in *Q. ilex* were measured leaves of the past year) of controls (Cnt; green bars) and trees grown under ALAN (Trt, orange bars). Means $\pm$ SD were subjected to a two-way ANOVA with treatment and timepoint as the source of variation. Means with different letters are significantly different after Fisher's LSD post-hoc test ($P \leq 0.05$). When the F ratio of the interaction between the variability factors was not significant, for each treatment, the means were subjected to one-way ANOVA with time as the source of variation; in case of non-homoscedastic data, a Welch ANOVA and Dunnett's T3 multiple comparison test were performed. Capital and Greek letters indicate statistically significant differences over time for controls and treated, respectively. For each timepoint, means were subjected to Student's *t*-test, and differences between treatments were indicated by asterisks ($P < 0.05$: *; $P < 0.01$: **; $P < 0.001$: ***) in case of non-homoscedastic data, a Welch *t*-test was performed.

Q. cerris it was high in ALAN-treated trees at all timepoints. Indeed, in the literature, there are many conflicting reports regarding the effect of streetlight illumination on leaf pigments of urban trees (Kwak et al., 2018; Li et al., 2019; Lo Piccolo et al., 2023, 2024; Sarala et al., 2013). Interactions between external light cues and the plant endogenous circadian clock regulate both chlorophyll biosynthesis and degradation. For instance, the light-dependent conversion of protochlorophyllide into chlorophyllide results in reduced chlorophyll production at night and enhanced synthesis during the day (Kobayashi and Masuda, 2019; Suzuki and Bauer, 1995). It is therefore plausible that ALAN interferes with this mechanism during both young and mature leaf stages, as also observed by Lo Piccolo et al. (2023). Indirect support for this hypothesis is provided by Liu et al. (2021), who reported, at the whole plant level, increased total N contents (but lower concentrations than controls) in *Acer truncatum* and *Quercus mongolica* exposed to white LED streetlamp (probably due to increased demand for N assimilation by the leaves). However, no specific studies have directly addressed this issue to date.

4.1.3. Autumnal and winter responses

Autumnal responses we reported revealed another layer of complexity in the interaction between ALAN and tree physiology.

During this season, a clearer and more consistent effect of ALAN emerged, particularly on leaf chlorophyll content in deciduous species. In *Q. cerris* and *L. styraciflua*, the higher midday net CO_2 assimilation and the maintenance of higher PSII efficiency (i.e., higher F_v/F_m and lower DI_0/CS_0 values) in senescing leaves indicate that ALAN delayed the progression of leaf senescence. This interpretation is further supported by higher values in leaf Chl_{index} in ALAN-treated trees, reflecting a delayed pigment degradation during this particular phenological stage, also resulting in a delayed leaf abscission for *L. styraciflua* and *Q. cerris* (Fig. S5). These results echo the pioneering observations of Matzke (1936), documenting the retention of green foliage in trees exposed to streetlights. Similar findings of greener leaves persisting longer under streetlamps have been repeatedly reported in urban contexts, both under HPS and LED illumination (Lo Piccolo et al., 2023; Lv et al., 2025; Meng et al., 2022; Škvareninová et al., 2017). The delay of the leaf senescence can be attributed to the alteration of natural light-dark cycles by ALAN, which can interfere with photoreceptor-mediated circadian rhythms and extend the perception of daylength (Meng et al., 2022). Indeed, plant photoreceptors such as phytochromes, cryptochromes, and phototropins play a central role in synchronizing circadian rhythms with external light cues, mediating seasonal transitions, and coordinating processes like flowering, senescence, and dormancy (Björn, 2015; Kong and

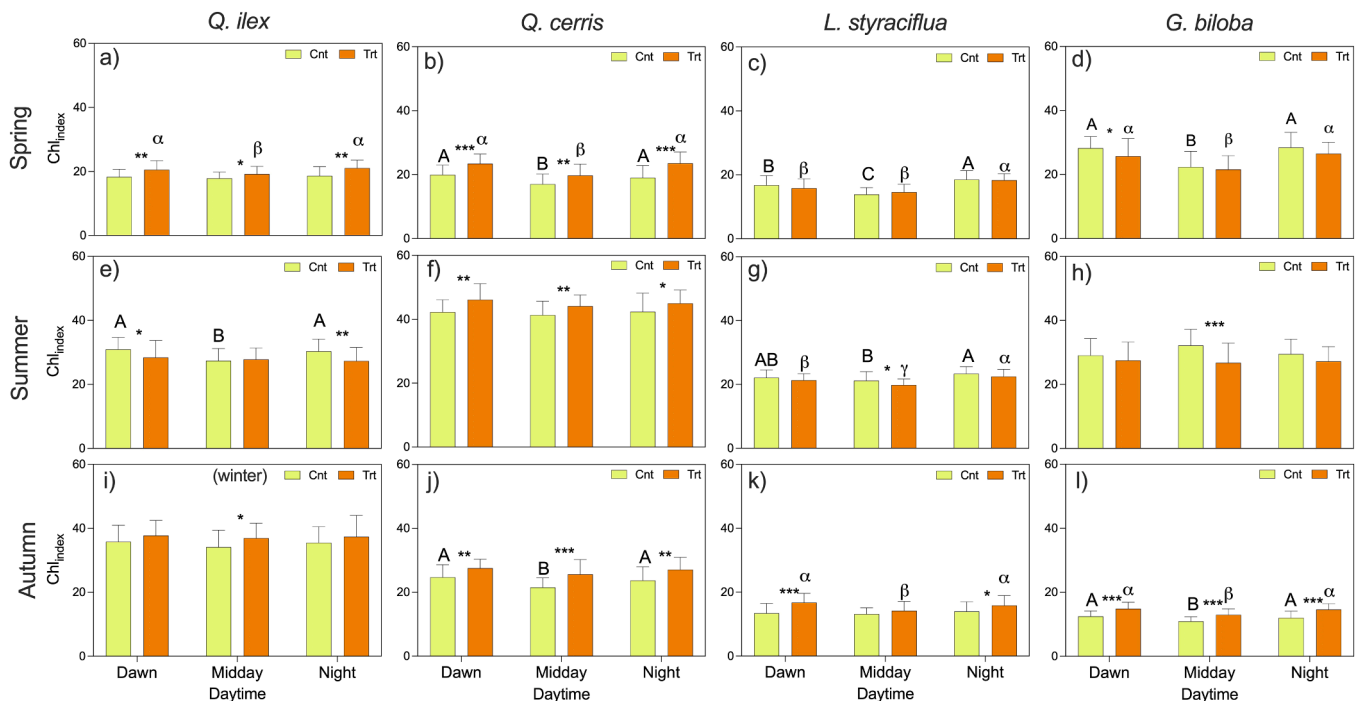


Fig. 7. Chl index ($\text{Chl}_{\text{index}}$) measured in spring, summer and winter/autumnal season, respectively, in *Q. ilex* (a,e,i), *Q. cerris* (b,f,j), *L. styraciflua* (c,g,k) and *G. biloba* trees (d,h,l); in *Q. ilex*, winter leaves were those of the past year. The parameters ($n = 30$) were measured at dawn, midday and night in leaves of controls (Cnt; green bars) and trees grown under ALAN (Trt; orange bars). Means $\pm$ SD were subjected to a two-way ANOVA with treatment and timepoint as the source of variation. Means with different letters are significantly different after Fisher's LSD post-hoc test ($P \leq 0.05$). When the F ratio of the interaction between the variability factors was not significant, for each treatment, the means were subjected to one-way ANOVA with time as the source of variation. Capital and Greek letters indicate statistically significant differences over time for controls and treated, respectively. For each timepoint, means were subjected to Student's *t*-test, and differences between treatments were indicated by asterisks ($P < 0.05$: *; $P < 0.01$: **; $P < 0.001$: ***), in case of non-homoscedastic data, a Welch *t*-test was performed.

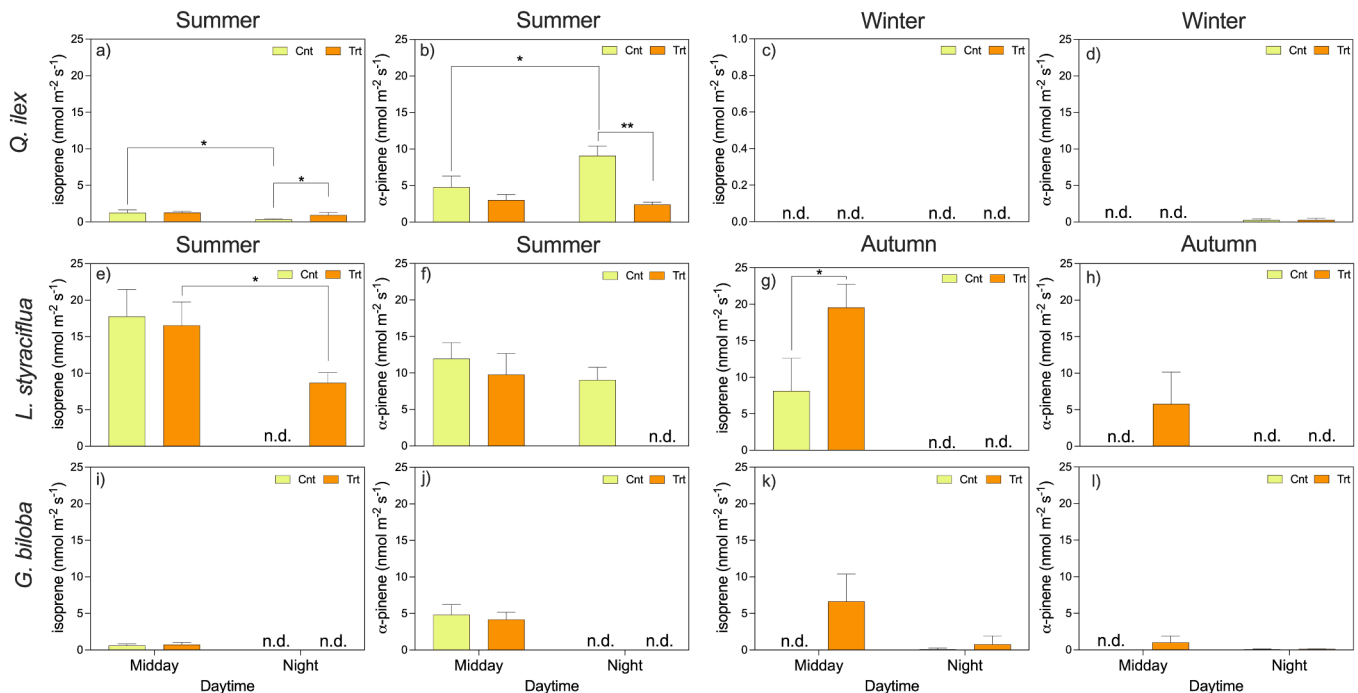


Fig. 8. Summer and autumnal (winter for *Q. ilex*) isoprene and α -pinene emissions measured in *Q. ilex* (a-d), *L. styraciflua* (e-h) and *G. biloba* (i-l) trees, respectively. Samples ($n = 3$ TD traps corresponding to three leaves from different plants) were measured at midday and night in leaves of controls (Cnt; green bars) and trees grown under ALAN (Trt; orange bars). For each timepoint and treatment, means $\pm$ SD were subjected to Student's *t*-test, and statistical differences were indicated by asterisks ($P < 0.05$: *; $P < 0.01$: **; $P < 0.001$: ***). In case of non-homoscedastic data, a Welch *t*-test was performed. N.d. means non-detected emissions.

Zheng, 2020). Nevertheless, the delay of the leaf senescence phenomenon under ALAN is not universal across tree species. Indeed, in

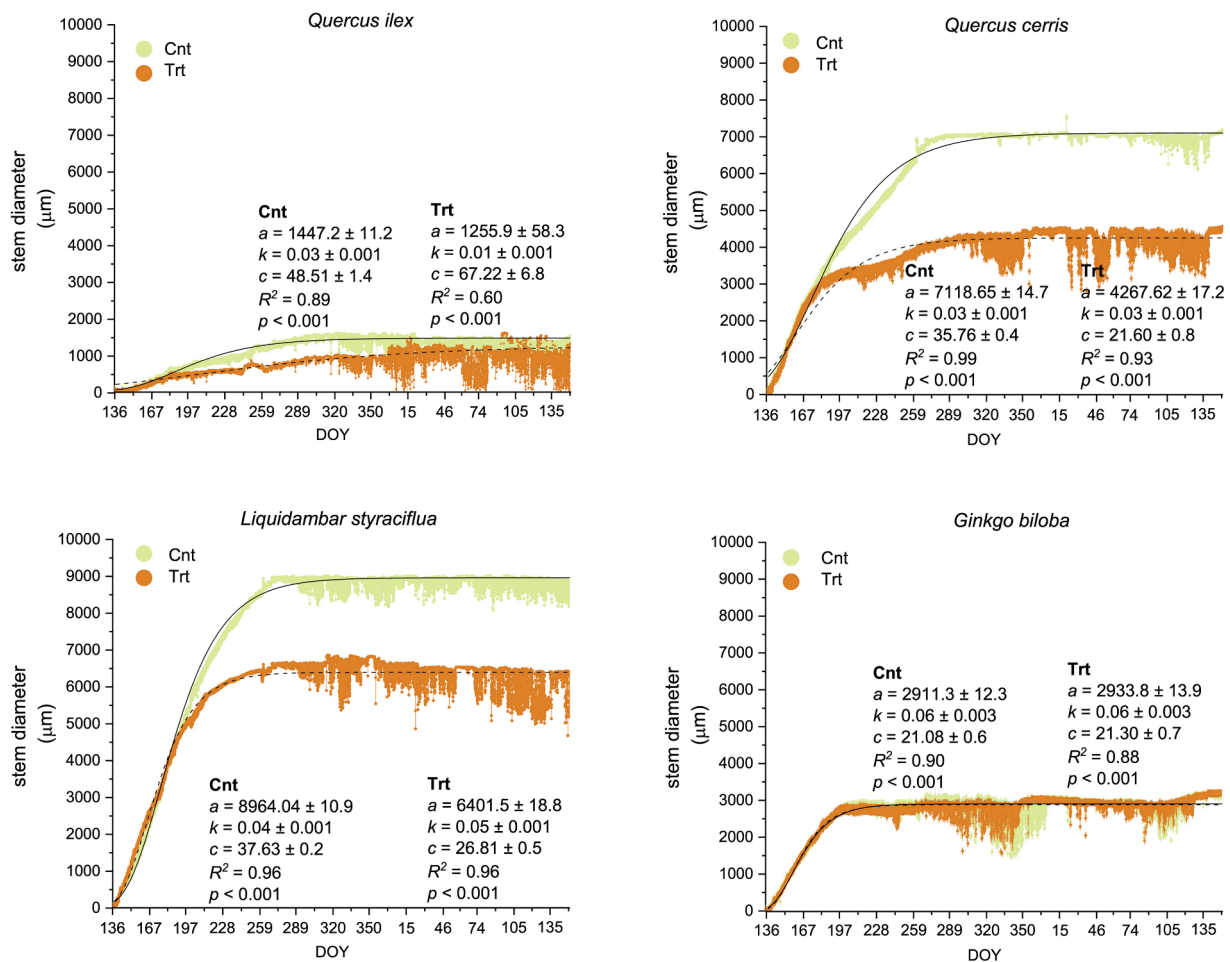


Fig. 9. Stem diameter in *Q. ilex*, *Q. cerris*, *L. styraciflua* and *G. biloba*, from May 2024 to May 2025 in control (Cnt, in green) and ALAN (Trt, in orange) conditions (values are mean of three replicates ± standard error). DOY indicates the day of the year. Time series of normalised stem diameter were fitted by Gompertz model functions (continuous line for Cnt and dashed line for Trt values) ($y = a - e^{-k(x-c)}$).

G. biloba, although ALAN-treated trees showed higher midday P_n , F_v/F_m , and Chl_{index} values (i.e., better preservation of photosynthetic functionality), the timing of leaf abscission remained unaltered (Fig. S5), indicating that in this relict species, this process is less sensitive to artificial light cues. Similar observations were reported for *T. platyphyllos* (Lo Piccolo et al., 2023) and *Betula pendula* (Sarala et al., 2013). Such interspecific variability may reflect differences in how tree species respond to environmental cues, since the onset of autumnal leaf senescence is modulated not only by photoperiod but also by temperature, or by the interplay between the two factors (Lian et al., 2021; Meng et al., 2022; Wang et al., 2025). However, recent satellite-based analyses of 428 Northern Hemisphere cities by Wang et al. (2025) further revealed that ALAN exerts a stronger effect than air temperature in extending the urban growing season, primarily by delaying its end. Overall, our autumnal results support the notion that ALAN promotes a prolonged onset of leaf autumnal senescence in deciduous species, sustaining physiological activity later in the season. However, the extent of this phenomenon is strongly species-dependent and may have ecological costs for ALAN-sensitive urban trees, such as potential altered nutrient remobilization due to retained leaves and increased vulnerability to frost damage due to active shoots during winter.

Winter conditions in seasonal environments pose a highly stressful challenge for evergreen plants due to low temperatures and other potential stressors that limit leaf photosynthetic activity (Niinemets, 2016a; Wyka and Oleksyn, 2014). Indeed, under prolonged cold, CO_2 assimilation is strongly downregulated, and evergreen species can face a

severe imbalance between light absorption and its utilization via metabolic pathways, forcing a shift toward leaf photoprotective strategies (i.e., sustained thermal dissipation, higher enzymatic antioxidant activity) (Verhoeven, 2014). Our results showed that *Q. ilex* displayed marked winter adjustments in photosynthetic responses, showing reduced P_n , g_s , F_v/F_m , and increasing DI_0/CS_0 values compared to summer results (see Table S1), supporting the previous research on this species (Martinez-Ferri et al., 2004; Martín-Sánchez et al., 2022; Pflug and Brüggemann, 2012). An open question, however, is whether ALAN can interact with these adjustments, and if so, through which mechanisms and at what times of day its effects are most pronounced. To our knowledge, this is the first study that analysed potential ALAN influences in an urban evergreen species during winter. During the winter season, *Q. ilex* exposed to ALAN exhibited reduced P_n and g_s , showing in terms of gas exchange a pattern partly comparable to that observed in summer, with lower dawn P_n values primarily attributable to stomatal limitations. During the night, a reduction of F_v/F_m was observed in ALAN-treated trees compared with the control. This nocturnal decrease in PSII efficiency may be attributed to ALAN, which, in combination with low nighttime temperatures, exacerbates the imbalance between light absorption and its metabolic utilization (i.e., very low nocturnal P_n values compared to summer; Table S1), thereby promoting a further down-regulation of the photosystem (Martinez-Ferri et al., 2004; Pflug and Brüggemann, 2012). In our case, the overlap of ALAN and cold stress likely intensified these responses, as indicated by the higher DI_0/CS_0 values, pointing to an enhanced activation of energy dissipation

pathways in Trt *Q. ilex* trees at night. Taken together, our results point to ALAN as a factor that can modulate winter photosynthetic responses in *Q. ilex*, potentially amplifying the constraints imposed by low temperatures.

4.1.4. ALAN influenced summer and autumnal BVOC emission

BVOCs are primarily synthesised via the chloroplastic methylerythritol phosphate (MEP) pathway, and are generally coupled to photosynthetic metabolism (Loreto et al., 1996; Sun et al., 2020). Summer can represent a critical period for BVOCs release, as elevated temperatures and high irradiance enhance isoprene biosynthesis and monoterpene volatilisation (Llusia et al., 2013). In this context, can ALAN influence the plant BVOCs emissions? Summer analyses showed that *Q. ilex* and *L. styraciflua* were significantly influenced by ALAN, emitting higher nocturnal isoprene levels than control trees, whereas *G. biloba* showed no significant response. To our knowledge, this provides the first experimental evidence that tree exposure to ALAN affects BVOCs emissions. Isoprene emissions are strongly light-dependent, typically increasing with irradiance and rapidly declining in darkness, which results in pronounced diurnal patterns closely linked to light availability (Wei et al., 2020; Zeng et al., 2025). The persistence of elevated isoprene emissions under ALAN likely reflects sustained light-driven chloroplastic metabolism at night, as also confirmed by gas exchange analyses data showing net CO₂ uptake in ALAN-treated trees. Such nocturnal illumination (outside the natural photoperiod) may generate transient imbalances between photosynthetic electron transport and the capacity of downstream metabolic processes to utilise reducing power and ATP (as suggested by summer night Φ_{Ro} reductions in *L. styraciflua*; i.e., a temporary mismatch between energy supply and metabolic demand) (Czaja and Kolton, 2026). Under these conditions, a more elevated isoprene may serve antioxidant functions, contributing to the buffering of transient chloroplastic redox perturbations and supporting thylakoid stability (Finì et al., 2017; Velikova et al., 2012; Vickers et al., 2009), even in the absence of detectable PSII photoinhibition. This interpretation is also consistent with Wang et al. (2024) reporting that chloroplast redox/energy status mediates the short-term regulation of leaf isoprene emission. Moreover, exposure to ALAN was associated with a reduction, and in some cases an inhibition, of nocturnal α -pinene emissions compared with control trees. These patterns may suggest that, under ALAN, a preferential channelling of dimethylallyl diphosphate (DMADP) toward isoprene synthesis may occur at the expense of monoterpene formation, resulting in reduced nocturnal α -pinene emissions (Vickers and Sabri, 2015).

On the other hand, in autumn, the higher midday isoprene and α -pinene emissions observed in the leaves of *L. styraciflua* and *G. biloba* compared to controls are likely the result of better preservation of photosynthetic and metabolic functionality (Niinemets et al., 2002), as also previously shown by physiological analyses. We are aware that the present results provide a partial view of the underlying mechanisms. Nevertheless, this study represents a first attempt to experimentally assess the effects of ALAN on tree BVOCs emission. Future studies should aim to disentangle the mechanistic basis of these responses by explicitly targeting MEP-pathway regulation and by considering additional stressors to ALAN (e.g., drought) that are increasingly a characteristic of urban environments. Such an integrated approach will be essential to better understand how urban infrastructures influence the role of urban vegetation in atmospheric chemistry under ongoing environmental change.

4.2. ALAN influenced tree radial stem diameter growth

Although the use of dendrometers is a common practice in forestry studies to assess radial growth dynamics of tree species (including *Q. ilex* or *L. styraciflua*) (McMahon and Parker, 2015), this is, to our knowledge, the first study to evaluate potential alterations of secondary growth induced by ALAN using continuous high-resolution dendrometer

monitoring. Our data revealed that stem diameter growth did not show damage, in terms of secondary growth, induced by ALAN conditions, due to a regular increase in the functions. In the autumn-winter season, daily stem variations described the dormant season, by not describing regular shrinkage, by being related to air temperature fluctuations and independently by water deficit or physiological processes (Cocozza et al., 2009). However, to note that ALAN negatively affects the secondary growth of *Q. ilex*, *Q. cerris* and *L. styraciflua*, detecting lower asymptotes of growth function in Trt than Cnt plants, especially during the summer period. Whereas in *G. biloba*, no differences were observed in secondary growth of Trt and Cnt plants, suggesting no direct impact of ALAN on the resource allocation for stem radial growth for this species. The reduction in radial growth observed in *Q. ilex*, *Q. cerris* and *L. styraciflua* may reflect altered carbon partitioning, consistent with the reduced gas exchanges observed during summer (July) in these species. Previous studies observed that ALAN can strongly influence gas exchange and tree morphological traits. For example, *L. tulipifera* exposed to HPS lamps exhibited reduced photosynthesis and decreased above-ground and belowground biomass production, indicating an impaired carbon balance under night lighting (Kwak et al., 2018). On the contrary, Liu et al. (2021) reported increased total biomass in *Q. mongolica* and *A. truncatum* grown under both white and red LED lamps compared to controls, while Lo Piccolo et al. (2024) observed enhanced branch biomass in *P. alba* exposed to ALAN. Both studies attributed these responses to the altered photoperiod induced by ALAN. The divergence between the species analysed in our study and those reported in previous research again underscores that ALAN effects are highly species-specific. However, in temperate regions, the period spanning from mid-May to mid-July represents the optimal growing season for deciduous and Mediterranean species like *G. biloba*. During this timeframe, the species likely undergoes vigorous cambial activity, driven by elevated photosynthetic rates and a concomitant increase in leaf-derived phytohormones, such as auxins and gibberellins (Bajguz and Piotrowska-Niczyporuk, 2023). Conversely, by mid-July, a physiological shift may occur: active radial cell division potentially ceases as resources are reallocated toward tissue maturation, lignification, bud primordia formation, and carbohydrate storage (Rathgeber, 2019). This transition is further exacerbated by rising summer temperatures and vapor pressure deficits (VPD), which trigger stomatal closure and consequently restrict expansive growth (Zailaa et al., 2025). However, as monitoring cambial dynamics was outside the scope of the present study, these physiological mechanisms remain speculative and warrant direct histological validation in future research. Moreover, in our study, during the late autumn, winter, and spring freeze-thaw cycles (spanning DOY 290–110), substantial stem diameter variations were consistently recorded as severe stem contraction. Biophysically, when temperatures drop below freezing, water is drawn out of the living cells to freeze within the intercellular spaces of the bark (Pearce, 2001). These extracellular freezing triggers a rapid collapse of the bark cells, resulting in a sudden, dramatic stem shrinkage of 1 mm or more within a single day (Zweifel and Häslar, 2000). Crucially, this contraction proved to be completely reversible once temperatures rose above freezing, reflecting the highly dynamic and elastic nature of the stem tissues under thermal and hydrological stress. Although this temporal pattern supports frost-induced stem shrinkage as a plausible explanation for the observed variations, the underlying tissue-level mechanisms were not directly assessed in the present study.

5. Conclusion

This work offered novel insights into how ALAN influences the physiological responses and growth rate of four widely planted urban trees (*Q. ilex*, *Q. cerris*, *L. styraciflua*, and *G. biloba*). By integrating measurements of leaf gas-exchange, chlorophyll a fluorescence, leaf chlorophyll index, BVOC emissions and stem radial growth, we found that seasonal responses strongly depended on species and leaf

developmental stage.

Q. ilex, *Q. cerris* and *L. styraciflua* were strongly influenced by ALAN during summer, when mature leaves exhibited reduced photosynthetic performance and an associated decline in stem growth. This denotes that chronic night lighting can translate from physiological disturbance into growth-level consequences. Moreover, *Q. ilex* and *L. styraciflua* showed enhanced nocturnal isoprene emissions, providing clear evidence that ALAN can increase BVOCs release during the nighttime period. This represents the first experimental evidence that ALAN can directly affect tree BVOC fluxes.

During autumn, leaves of *Q. cerris* and *L. styraciflua* exposed to ALAN maintained photosynthetic functionality and exhibited delayed senescence, indicating that ALAN can alter tree phenology.

The effects of ALAN on the photosynthetic machinery were also evident during winter, as shown by the alterations detected in the evergreen *Q. ilex* both at night and in the early morning.

Overall, *G. biloba* was the least responsive to ALAN among the tree species analysed, showing detrimental effects mainly during early leaf development. On the contrary, no consistent alterations were observed in mature leaves during summer, and no delay in leaf abscission time was observed in the autumnal season. This suggests the potential suitability of this species for moderated illuminated urban settings.

Across species, the chlorophyll fluorescence parameter Φ_{Ro} emerged as a consistent response indicator of ALAN-induced alterations, proposing its utility for rapid screening and monitoring approaches.

However, this study analysed a relatively short exposure period compared to the lifelong pressure experienced by trees in real urban settings, where chronic ALAN could lead to acclimation, cumulative damage, or altered physiological responses. Therefore, future long-term studies should be conducted under actual field conditions to fully comprehend these responses in real-world urban environments.

The pronounced species-specificity of the responses observed underscores the need to develop species-specific sensitivity tables to ALAN and the creation of a potential disturbance index. Such tools would support more informed tree selection and adaptive lighting design in urban environments, ultimately contributing to the resilience, ecological functionality, and sustainability of urban ecosystems under increasing artificial nighttime illumination.

CRedit authorship contribution statement

Ermes Lo Piccolo: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Barbara Mariotti:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Sara Beltrami:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Valentina Lazazzara:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Francesca Alderotti:** Writing – review & editing, Investigation. **Cecilia Brunetti:** Writing – review & editing, Methodology, Investigation. **Claudia Coccozza:** Writing – review & editing, Methodology, Investigation. **Andrea Baptista:** Writing – review & editing, Investigation. **Antonella Gori:** Writing – review & editing. **Alberto Maltoni:** Writing – review & editing. **Francesco Ferrini:** Writing – review & editing, Project administration, Funding acquisition.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.ufug.2026.129716](https://doi.org/10.1016/j.ufug.2026.129716).

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