urban science

Review

Artificial Light at Night (ALAN) as an Emerging Urban Stressor for Tree Phenology and Physiology: A Review

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Abstract: Artificial light at night (ALAN) is an expanding environmental issue, particularly in urban areas. This review aimed to present the state of the art regarding the impact of ALAN on specific and interrelated aspects related to physiological processes and life cycle events in tree species. The reviewed studies highlighted the multifaceted effects of artificial light on plants, offering insights and perspectives to guide future research in this evolving and stimulating field. ALAN disrupts circadian rhythms, alters photoperiodic responses, and affects photosynthesis and carbohydrate metabolism. Changes in phenology such as delayed senescence and altered budburst timing demonstrated species-specific responses, often compounded by other urban stressors like heat and drought. Despite an increased interest, knowledge gaps remain concerning the species-specific responses and the effects of light spectra as well as the long-term consequences on tree physiology. These gaps highlight the need for integrated research approaches and urban planning strategies to mitigate ALAN effects, ensuring the resilience of urban trees and preserving ecosystem services in the context of growing urbanization and climate change.

Keywords: high-pressure sodium lamps (HPS); light-emitting diode lamps (LED); plant phenology; plant physiology; photopollution; urban vegetation

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Academic Editors: Francesco Ferrini, Ermes Lo Piccolo, Barbara Mariotti and Luis Hernández-Callejo

Received: 11 November 2024
Revised: 27 December 2024
Accepted: 7 January 2025
Published: 10 January 2025

Citation: Friulla, L.; Varone, L. Artificial Light at Night (ALAN) as an Emerging Urban Stressor for Tree Phenology and Physiology: A Review. *Urban Sci.* **2025**, *9*, 14. https://doi.org/10.3390/urbansci9010014

1. Introduction

Over the last century, the rapid expansion of urban land has led to a range of environmental challenges, including habitat fragmentation, rising temperatures, drought, and the pollution of the different environmental matrices [1–4]. Urban stressors can cause significant damage to living organisms, and the most worrying element linked to them is their multiplicity and, often, their simultaneous action [5]. In recent years, another urban stress factor has become apparent: the ever-increasing presence, intensity, and type of lighting on urban streets [6–9]. Light pollution can be defined as an alteration of natural light during the night period caused by anthropogenic activities [10]. It is one of the most widespread forms of environmental pollution, as it occurs even in locations that have not been significantly altered by other types of human activity [10]. The use of artificial light in cities is increasing by 6% every year [6]. Along with this quantitative growth in artificial lighting, the areas requiring illumination have also expanded. Beyond streetlamps, the rising number of commercial establishments, security lights, and vehicles further demonstrates this growing trend [6].

In the past, urban areas were predominantly illuminated with high-pressure sodium (HPS) lamps, which, however, in recent years have been largely replaced with light-emitting diode (LED) lamps [8,11] with different functioning characteristics (Figure 1).

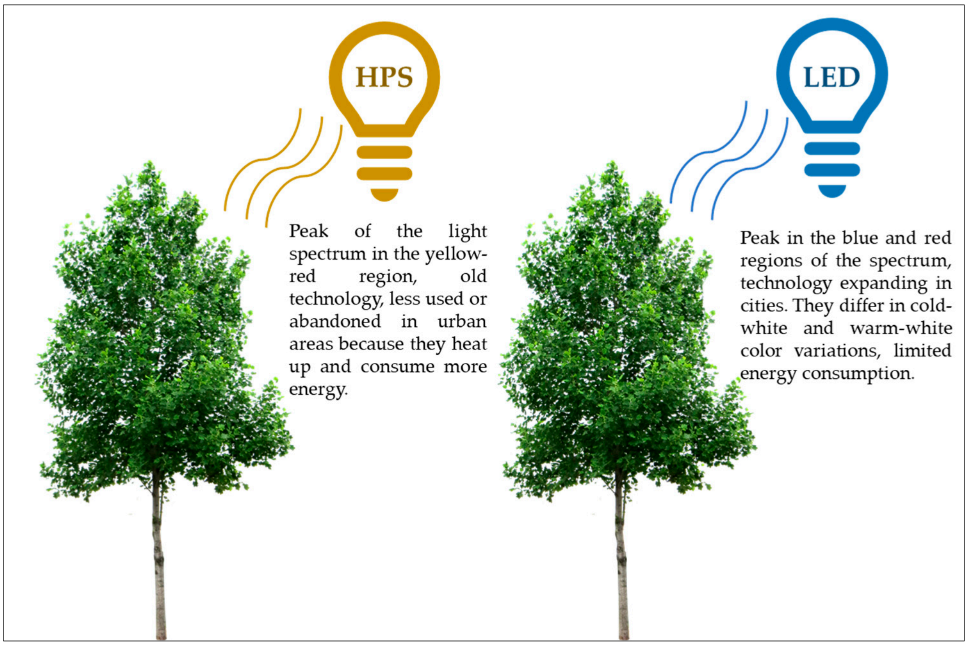

Figure 1. Main difference between high-pressure sodium (HPS) and light-emitting diode (LED) lamps.

An increasing number of cities worldwide are rapidly replacing HPS lamps with LED ones to align with the "Smart City" standard [12]. The objective of this initiative is to enhance efficiency, sustainability, livability, and overall quality of life through the application of technology and data-driven solutions [12].

The significant impact of LED lamps in terms of low consumption (about 65 W at a current of 350 mA compared to 170 W for HPS) and savings is a significant factor [11]. In addition, they take up less space and have a longer lifespan, about 50,000 h [13] as well as being easier to dispose of [12].

The regulation of vital processes is dependent upon the presence of light, which is essential for the functioning of most living organisms. Studies on light pollution and the effects of urban street lighting on organisms date back to the 1980s [14]. In line with the growing global population and concomitant increase in urbanization, interest in light pollution and artificial light sources in cities has increased during the 21st century. This has led to many studies worldwide which have produced significant insights into the effects of artificial light in cities [15–17]. However, despite a growing interest in studying how light pollution affects organisms, information is often still fragmented and variable [10].

In recent years, an emerging topic within studies on urban light pollution concerns the effects of artificial light at night (ALAN) on plants [6–9]. Growing evidence suggests that in urbanized areas, the continuous exposure of plants to ALAN coupled with the other stress factors typical of cities, such as heat, drought, and soil compaction [18–21], represent a significant new threat to plant health [22–24].

Plants perceive light through photoreceptors, which enable them to detect the duration, intensity, quantity, and quality of light. Photoreceptors include phytochromes, UV-A, phototropin, UV-B, and green light receptors [6]. In the context of plant biology, light represents a critical ecological factor, serving as the primary energy source for the photosynthetic process, which is the foundation of plant metabolism. Light serves also as an environmental signal. Its intensity, duration, and spectral distribution are crucial for enabling plants to perceive diurnal cycles, seasonal variations, and environmental characteristics, thereby allowing them to regulate their physiological activities effectively [24]. In plants, light therefore has a pivotal role not only in photosynthesis but also in regulating morphogenesis, movements (tropisms), and biological rhythms (circadian rhythm) [25]. However, an excess of light can damage the photosynthetic apparatus, inhibit physiological activities, and shift a phase in the circadian clock [6,26,27].

The impact of artificial light on plants is influenced by several parameters, including the direction and distance of the light and its intensity, distribution, modulation, and polarization. The type and use of lamps also play a significant role. It has been previously observed that the use of HPS lamps delayed the onset of leaf senescence in deciduous species in autumn [28–30]. Early budding [31,32], alteration in chlorophyll fluorescence [7,27], and issues with the dynamics of soluble and non-soluble fractions of non-structural carbohydrates have also been observed [19,20,24]. However, several key knowledge gaps remain, especially concerning the physiological impacts of different lighting technologies such as HPS and LED lamps. Since evaluations of the effects of artificial light exposure on plants began before the advent of LED technology, there is currently no research comparing the impact of HPS [29,30,32] and LED lamps on plant species [7,11,22–24,26,27,31,32]. Consequently, it cannot be stated with certainty which of these two technologies is more harmful to plants.

This review aimed to present the state of the art regarding the impact of artificial light on specific and interrelated aspects of plant functioning such as phenology, physiology, and carbohydrate dynamics. Although experimental studies in this field are becoming increasingly common, comprehensive reviews remain scarce. Thus, this review wanted also to provide researchers with an up-to-date resource by synthesizing and compiling recent experimental findings.

2. Data Source

The preparation of this review involved a systematic selection of literature to evaluate the degree and growth of academic interest in light pollution over time. Early research primarily focused on light pollution as a general phenomenon, particularly its prevalence in urban areas. Over time, interest has expanded to explore the environmental impacts of artificial light, especially its effects on wildlife. Relevant studies point up how light pollution affects human health and the behavior and migration patterns of other animal species such as birds, sea turtles, and mammals [33–36]. In recent years, attention has shifted toward understanding how artificial light impacts plant species.

For this review, the articles were identified through an extensive search carried out via the SCOPUS database by using keywords such as “light pollution”, “artificial light effects”, “photopollution”, and “urban ALAN”. The research produced approximately 80 papers published between 1980 and 2024. However, according to the specific objective of this review, about 37 papers with a particular focus on the alteration of plant physiology and phenology during nighttime were selected. Overall, 27 species were analyzed, whose characteristics in terms of taxonomy, growth form, leaf habitus, and ecological light requirements [37–61] are shown in Table 1.

Table 1. Characteristics of considered species in the reviewed studies.

Species	Family	Habit	Leaf Habitus	Exposition	Reference
Fagus sylvatica	*Fagaceae*	Arboreal	Deciduous	Shade-tolerant	[37]
Acer campestre	*Aceraceae*	Arboreal	Deciduous	Heliophilous	[38]
Tilia tomentosa	*Tiliaceae*	Arboreal	Deciduous	Shade-tolerant	[39]
Kerria japonica	*Rosaceae*	Shrub	Deciduous	Shade-tolerant	[40]
Spiraea x *cinerea*	*Rosaceae*	Shrub	Deciduous	Shade-tolerant	[41]

Table 1. *Cont.*

Species	**Family**	**Habit**	**Leaf Habitus**	**Exposition**	**Reference**
Cornus alba	*Cornaceae*	Shrub	Deciduous	Shade-tolerant	[42]
Platanus x *acerifolia*	*Platanaceae*	Arboreal	Deciduous	Heliphilous	[43]
Tilia platyphyllos	*Tiliaceae*	Arboreal	Deciduous	Heliophilous	[39]
Rosa hybrida	*Rosaceae*	Shrub	Deciduous	Heliophilous	[44]
Oryza sativa	*Poaceae*	Herbaceous	Annual	-	[45]
Aesculus hippocastanus	*Sapindaceae*	Arboreal	Deciduous	Heliophilous	[46]
Alnus glutinosa	*Betulaceae*	Arboreal	Deciduous	Heliophilous	[47]
Betula pendula	*Betulaceae*	Arboreal	Deciduous	Heliophilous	[48]
Fraxinus excelsior	*Oleaceae*	Arboreal	Deciduous	Heliophilous	[49]
Quercus robur	*Fagaceae*	Arboreal	Deciduous	Heliophilous	[50]
Tilia cordata	*Tiliaceae*	Arboreal	Deciduous	Heliophilous	[39]
Arachis hypogaea	*Fabaceae*	Herbaceous	Annual	Heliophilous	[51]
Licopersicum esculentum	*Solenaceae*	Herbaceous	Annual	Heliophilous	[52]
Terminalia catappa	*Combretaceae*	Arboreal	Deciduous	Heliophilous	[53]
Holoptea integrifolia	*Ulmaceae*	Arboreal	Deciduous	Heliophilous	[54]
Bauhinia variegata	*Fabacee*	Arboreal	Deciduous	Heliophilous	[55]
Rhus typhina	*Anacardiaceae*	Arboreal or shrub	Deciduous	Heliophilous	[56]
Lonicera pileata	*Caprifoliaceae*	Shrub	Evergreen	Heliophilous	[57]
Euonymus japonicus	*Celastraceae*	Shrub	Evergreen	Heliophilous	[58]
Saraca asoca	*Caesalpinaceae*	Arboreal	Evergreen	Heliophilous	[59]
Thevetia peruviana	*Apocynaceae*	Shrub	Evergreen	Heliophilous	[60]
Ficus benjamina	*Moraceae*	Arboreal	Evergreen	Shade-tolerant	[61]

The selected articles were critically examined to understand the research motivations, contextual factors, study locations, and experimental control protocols.

3. The Impact of Artificial Lighting on Plant Circadian Rhythms and Ecosystem Dynamics

Among the processes under light control in plants, the circadian rhythm is crucial, as plant evolution is closely aligned with the natural light cycles that serve as critical signals for regulating plants' metabolic functions, growth, and development. Circadian rhythms are biological cycles that follow an approximate 24-h period [62]. The circadian rhythm is pivotal in synchronizing physiological processes, with environmental signalling being linked to daily temperature and light/dark cycles [63]. The circadian clock is the basis of many plant processes such as photosynthesis, stomatal behaviour, flowering, and hormone production [64,65]. In plants, this internal clock is synchronized with the natural day–night cycle through the detection of light by photoreceptors, including phytochromes and cryptochromes, which are sensitive to red/far-red and blue light, respectively [17,64]. Circadian rhythms enable plants to anticipate daily and seasonal changes, optimizing their metabolic and growth functions in response to environmental cues.

All the components of this cycle are finely regulated at a genetic level by the light-regulating genes, which play a fundamental role in the perception of light by the plants and consequently influence its rhythm [66]. For instance, in *Arabidopsis thaliana*, high flowering under long-day conditions is triggered by activating a specific florigen gene whose promoter binds to a specific transcription factor, which ensures that the florigen gene is activated specifically under long-day conditions [67]. This transcription factor works as a timer controlled by the circadian clock, and its protein levels increase in response to light [68].

As an endogenous regulation with a delicate balance, the circadian clock remains constant and free from specific changes when environmental conditions such as light and temperature remain unchanged. Accordingly, it can be inferred that an over-dimensioned exposure time to artificial light can have a detrimental impact on the circadian cycles, leading to desynchronization with the environment and resulting in the shift of all the plant activities associated with it [66]. In particular, the exposition to ALAN disrupts the intrinsic circadian rhythms of plants, leading to a cascade of effects throughout different levels of organization from altered gene expression to ecosystem level.

It has been reported that night lighting, especially in the red and far-red spectra, affects photoperiodic responses, which are crucial for determining flowering time [17]. In turn, changes in flowering times induced by ALAN may misalign with the activity patterns of nocturnal pollinators, reducing pollination success and threatening plant–pollinator mutualisms [69]. Additionally, altered growth rates and resource allocation caused by light pollution can influence plant competition and succession, reshaping plant community structure and, thereby, ecosystem functioning.

4. Effect of ALAN on Plant Phenology

Plant phenology is defined as the science that studies the seasonal sequence of the plant life cycle, which plays an important role in understanding the health and metabolic functioning of plants, as well as in elucidating plant–environment interactions [70,71]. Plant phenology is controlled by several factors. While air temperature is the dominant factor regulating phenological events, photoperiod and light exposure also play a critical role. Together, these factors interact in a dynamic and complex manner to determine the timing of various phenological events including budburst, flowering, fruiting, and leaf senescence [71–73]. This enables plants to respond adaptively to climatic variations and ecological pressures, thereby optimising survival and reproduction across diverse habitats. Anthropogenic influences such as ALAN due to streetlamps are introducing new challenges. Indeed, ALAN may extend the photoperiod, alter the light intensity, and shift the spectral quality of illumination [71,73]. The effect of ALAN may lead to mismatches among the different phenological phases in accordance with several studies. Nevertheless, the reported findings may appear confounding due to species-specific and treatment-specific responses. Specifically, research carried out in the field and under controlled conditions indicated that in both cases, the ALAN exposure translated into a delayed leaf senescence and accelerated bud burst [28,32,74].

In a study on the spring phenology [32] of eight deciduous species, two levels of LED light intensity at night were used (Table 2). Branches with shoots were placed inside specific chambers and subjected to 3 artificial light treatments namely Control (C), Moderate Light Pollution (M-LP), and finally Low Light Pollution (L-LP). The results highlighted that all the species showed a variation in the phenological timing and the different phases of leaf development in spring as well as in the groups exposed to the two intensities compared to the control group. In the majority of cases, the acceleration of phenological times was observed in the group subjected to L-LP treatment. However, this was not the case for *Fagus sylvatica* and *Acer campestre*, which showed phenological acceleration under M-LP treatment. These inconsistencies between plant behavior in response to ALAN highlight the need for further controlled studies to clarify the mechanisms driving differential responses, while also considering that while many studies indicate ALAN disrupts phenology, others have reported minimal or no significant effects of streetlamps on plant behavior. For instance, the exposure of *Betula pendula* to artificial light did not cause an alteration in the phenological phases [75]. This latter study began in spring after a sharp drop in temperature, and it was carried out on 21 individuals with reddened leaves and 21 individuals with green leaves growing in urban avenues. The classification was also based on the distance of streetlamps (Table 2). Sampling and analysis continued in the autumn, with the main objective of understanding whether there were any delays in the degradation of pigments (chlorophyll a and b and carotenoids) associated with leaf senescence. No significant differences were found based on the distance from the streetlamps, and consequently no delay in the onset of foliar senescence in *Betula pendula* associated with ALAN. Probably, this outcome was attributable to the insufficient light intensity to which the plants were subjected, which was insufficient to induce a stress response that would alter the natural timing of senescence.

As previously stated, plant phenology is controlled by several ecological factors. Consequently, it is possible to infer that the phenological response to ALAN is influenced by its interaction with other environmental drivers, such as temperature. Valuable insights into the synergistic effect of artificial light pollution and temperature increase on phenology were reported in [76]. In this research, the leaf-out and flowering of seven tree species (*Aesculus hippocastanus*, *Alnus glutinosa*, *Betula pendula*, *Fagus sylvatica*, *Fraxinus excelsior*, *Quercus robur*, *Tilia cordata*) were carried out. Two datasets (nighttime light and temperature datasets) were analyzed over the period of 1991 to 2015 in different areas of Central Europe, which were classified considering the quantity and stability of light (Table 2). Over this time, it was observed that 70% of the sites present in both datasets showed an increase in the presence of artificial light from 1991 to 2015. This increase was significantly correlated with a delay in leaf-out across the studied species, with the extent of the delay varying by species. *Tilia cordata* and *Quercus robur* showed a 12% delay, *Fagus sylvatica* 15%, *Fraxinus excelsior* 19%, *Betula pendula* 23%, *Aesculus hippocastanum* 20%, and *Alnus glutinosa* 39%. The results indicate that the phenological progression of plants in areas with higher levels of artificial light was significantly hindered. These outcomes are particularly concerning, as they suggest that ALAN, when combined with temperature increases, exacerbates disruptions to natural phenological cycles. Such alterations may have effects on broader ecological processes, including shifts in herbivory, pollination timing, and resource allocation in ecosystems.

Most of the research carried out on the effects of ALAN on plant phenology has focused on individual plants, particularly those found in urban streets. However, it is also worth analyzing the relationship between ALAN and phenology at a broader spatial scale. In this regard, the impact of ALAN on spring phenology in the USA was evaluated across a substantial geographical area [77]. This study incorporated a wide range of species as opposed to studying individual plants. Data over a long period (2001–2013) were analyzed using the MODIS Land Cover Dynamics Product platform (MCD12Q2, Collection 6), which provides annually updated data. From this database, it has been possible to extract values corresponding to greening data, which highlighted the beginning of the growing season. The night luminance data were recorded with the Defense Meteorological Satellite Programme Operational Linescan System, and the daily weather data was also recorded with Daymet (version 2). Observations indicated that ALAN advanced the start date of the growing season, although this effect varied spatially. Specifically, ALAN exhibited a propensity to advance the growing season in regions characterized by moderate climates, while its influence was less pronounced, or even exhibited a reverse effect, in regions experiencing very high or very low temperatures. The reasons for the greater impact of ALAN in climatically moderate regions are not yet fully understood. However, the differing strategies of plant resistance to climate change and their association with photoperiod were likely to be significant factors. This is particularly evident in late-succession species and those found in other latitudes. These findings serve to underscore the view that climatic factors interact with the action of artificial light itself. The persistence of mild winters and warm springs, coinciding with the presence of ALAN, has been identified as a contributing factor to the observed lengthening of the photoperiod, resulting in a considerable advance in the growing season. Furthermore, a distinction has been made between urban and non-urban areas [77]. It was found that there were no significant differences between the two areas. This can be attributed to the fact that, despite the reduced significance of ALAN exposure, it still exerted an influence on the phenological timing, probably due to the short distance to urban areas.

On the other hand, autumn phenology covers all those processes that prepare the plant for dormancy in the winter period [78]. As in spring phenology, in this case it has also been hypothesized and demonstrated that exposure to artificial light during the night hours could modify the timing of the leaf senescence process, resulting in a delay in leaf fall compared to natural times [28,29]. The autumn phenology and all the processes associated with it have received significantly less attention from researchers than spring phenology. However, an analysis of the existing literature indicates that in relation to primary climatic factors, autumn phenology may be influenced by ALAN [79,80]. The effects of ALAN on both autumn (through leaf coloring) and spring (by opening buds) phenology on a global scale by using the NASA Black Marble ALAN (version 1.2) was studied in [81]. Phenology data on plants in the USA were analyzed from 2011 to 2016 with the USA National Phenology Network. The results of this research confirmed previous studies: in 73.3%, the opening of the buds took place with an advance of about 9 days in sites with artificial light presence. In the case of senescence, there was an average delay of about 6 days in plants at sites where ALAN was present. The correlation between the actual presence of ALAN and temperature was also determined, and a positive correlation between the delay in the senescence process and the synergistic action of ALAN-temperature was noted. This correlation was not recorded for the spring phenology and therefore in the process of opening the buds. These two conditions (temperature rise and ALAN) are increasing in the urban areas of the world [81]. Thus, understanding the effect of this synergy on phenological but also physiological aspects is crucial to have clear responses of plant species that remain in the city and understand today's answers but also try to create future predictive models that have as context warmer and brighter nights [81].

Leaf senescence represents the final phase of leaf development. The process is distinguished by a range of internal and external phenomena, which are contingent upon variables such as the age of the plant, the mobilization of phytohormones, and the presence or absence of environmental stress [82].

The regulation and synthesis of endogenous hormones directly involved in the plant senescence process can be influenced by temperature and daylight hours. Low temperatures and a few hours of light determine a negative correlation with the regulation of abscisic acid, which increases as the temperature and length of day decrease. By contrast, zeatin riboside and gibberellins decrease in such conditions. Having this awareness is very important because it allows us to consider both natural and artificial mechanisms, such as ALAN, which may have a synergistic action that directly affects phenology and that today needs an experimental extension [80].

In deciduous plants frequently used in European cities for urban greenery, the onset of the specific phases of autumn phenology began with a delay of approximately 20 days and lasted at least a week longer [28], with an extension of the coloring and leaf fall time by six to seven days (Table 2). The negative effects were recorded mostly in the canopy points of both plants directly exposed to lighting. It is important to consider that the species taken into consideration in this study were defined as particularly sensitive to light, and their responses were similar for exposure to both LED and HPS lamps. However, the extent of the difference between the effects of LEDs and HPS was not specified. As already mentioned, variable temperature and climate trends should be taken into account during the analysis of phenological patterns. Furthermore, monitoring the total amount of light (lx) in the study locations provides a clearer picture of the conditions and contexts under consideration. In adverse weather conditions characterized by cloudy skies and high air humidity, light pollution shows higher values, from a minimum of 1.8 lx to a maximum of 8.5 lx, while in clear sky conditions the minimum values are about 1.1 lx and the maximum values are 6.5 lx. This phenomenon is due to a higher light reflectance in conditions characterized by a higher level of water and aerosols [28]. According to the CIE (International Commission on Illumination), the amount of light that can be considered light pollution after curfew is 11 lx [83].

Another study on autumn phenology involved individuals of *Platanus* x *acerifolia* exposed to HPS lamps in uncontrolled urban conditions [29]. The phenological protocol used in this study was based on presence–absence, which is the most realistic approach in similar study conditions (Table 2). The presence of green leaves in the plants exposed to light, as well as in the exposed parts of the foliage, was found to be a higher percentage than in the unexposed plants and in the unexposed parts of the foliage.

Table 2. Description of treatments and effects on phenology in response to different lamp types.

Type of Illumination	Species	Treatment and Set-Up	Effects	Reference
LED	*Tilia tomentosa*, *Betula pendula*, *Fagus sylvatica*, *Acer campestre*, *Cornus alba*, *Lonicera pileata*, *Kerria japonica*, *Spiraea* x *cinerea*	C: shoots for 12 h at 100 mmol m^{-2} s^{-1} and for 12 h at 0 mmol m^{-2} s^{-1} M-LP: shoots for 12 h at 100 mmol m^{-2} s^{-1} and 12 h at 30 mmol m^{-2} s^{-1} of light. L-LP: shoots for 12 h at 100 mmol m^{-2} s^{-1} and 12 h at 1 mmol m^{-2} s^{-1}	L-LP: acceleration of phenological times in six species M-LP: acceleration of phenological times in *F. sylvatica* and *A. campestre.*	[32]
High-pressure mercury	*Betula pendula*	Urban street, red-emerging leaves near streetlamp (SLR) and farther away from (CR) and green-emerging leaves near streetlamp (SLG) and farther away from (CG)	No significant difference between treated and control	[75]
NA (dataset sky luminance)	*Aesculus hippocastanus*, *Alnus glutinosa*, *Betula pendula*, *Fagus sylvatica*, *Fraxinus excelsior*, *Quercus robur*, *Tilia cordata*	Nighttime light, temperature and phenological (autumn) dataset in the period 1991 to 2015 in areas of Central Europe	*T. cordata* and *Q. robur* showed a 12% delay, *F. sylvatica* 15% delay, *F. excelsior* 19% delay, *Betula pendula* 23% delay, *A. hippocastanum* 20% delay, and *A. glutinosa* 39% delay	[76]
NA (dataset sky luminance)	-	Nighttime light, temperature and phenological (spring) dataset in the period between 2001 and 2013 in the USA	Spring phenological anticipated Urban area vs. non-urban area, no significant differences Major influence on temperate areas	[77]
NA (dataset sky luminance)	-	Nighttime light, temperature and phenological (autumn and spring) dataset in the period between 2011 and 2016 in the USA	Spring phenological anticipated Leaf autumnal senescence delayed	[81]
LED	*Euonymus japonicus*, *Rosa hybrida*	Plants exposed to LED controlled by a light-sensitive switch at night	Soluble sugar and starch content in plants exposed > unexposed plants	[23]

Table 2. *Cont.*

Type of Illumination	Species	Treatment and Set-Up	Effects	Reference
HPS, LED	*Acer pseudoplatanus* *Rhus typhina*	3 urban areas with HPS lamps with spherical diffusers and top covers and LED lighting with flat diffusers	Delay in autumnal phenological phases in the specific parts of exposed canopy	[28]
HPS	*Platanus* x *acerifolia*	3 different sites (A, B, C) and presence–absence protocol	Presence of green leaves in exposed plants > in unexposed plants	[29]

5. Effects of ALAN on Plant Physiology and Carbohydrate Dynamics

The exposure to artificial night light stimulates and sustains the photosynthetic process during periods when the natural cycle would otherwise cease. This unusual activity therefore results in a series of disruptions to the physiological activity of the plants, which are harmful to plant functioning.

Some studies have highlighted the presence of impaired net photosynthesis values, both in plants exposed to LED light and in plants exposed to HPS compared to control plants [11,23,24,29,84]. In plants such as *Tilia platyphyllos* and *Platanus* x *acerifolia* exposed to artificial light treatments [11], significant variations were noted compared to the control group, especially in the growing season and in analyses carried out at night and at sunrise (Table 3).

The groups exposed to a light intensity of 300 mmol m^{-2} s^{-1} and 700 mmol m^{-2} s^{-1} showed significant differences in net photosynthetic rate compared to the control group, regardless of treatment of applied light. Stomatal conductance values were statistically significant only on a seasonal basis and at sunrise. This study also demonstrates how exposure to artificial light at night resulted in photosynthetic activity at atypical times in both *Tilia platyphyllos* and *Platanus* x *acerifolia* trees.

Plants exposed to artificial night light exhibited positive values of net photosynthetic rates at night. Conversely, at dawn, they showed a lower net photosynthetic rate than plants not exposed to artificial light. The decline in photosynthesis at dawn was attributed to the inefficiency of the light-harvesting antenna complexes. This phenomenon was not observed in control plants, which had undergone the appropriate nighttime “rest” and demonstrated a greater efficiency in electron transport.

Furthermore, the intercellular CO_2 concentration was lower in the plants exposed to artificial light than in the control plants during the nighttime. The presence of low values of intercellular CO_2 concentration at night can be related to the mobilization of CO_2 for photosynthetic purposes. This was also supported by the lack of significant differences between control and exposed plants in stomatal conductance. This demonstrated how photosynthetic efficiency does not depend on stomatal limitations, a case that was also demonstrated in [29].

Another case in which the net photosynthetic efficiency of plants exposed to nighttime artificial light decreased due to stomatal limitations was described in *Arachis hypogaea* [85]. In this study, plants subjected to 24-h light showed a greater stomatal inefficiency than those subjected to artificial lighting for 12 h (Table 3).

A significant reduction of the net photosynthetic rate and stomatal conductance occurred also in *Euonymus japonicus* and *Rosa hybrida* [19] exposed to artificial light (Table 2). In this experiment, plants were subjected to multi-stress conditions such as continuous artificial light, drought, and a combination of both conditions. Under adverse conditions, plants implemented responses to survive or limit damage as much as possible.

The decrease in net photosynthetic rate was due to stomatal factors or to the inhibition of PSII activity, which we indicate as photoinhibition. The rhythm of chlorophyll production and breakdown is regulated by the interaction between the external light signal perceived by the plant and its circadian rhythm. The few studies aimed to analyze the effects of an artificial light night on chlorophyll production are often conflicting.

Some studies [11,86] have reported that if plants were exposed to light at night and the ratio of red/blue light, which is usually involved in chlorophyll biosynthesis, was similar to that present during daytime hours, the amount of chlorophyll present at night increased. By contrast, other studies [23,87] carried out in the *Cymbidium* genus and on *Euonymus japonicus* and *Rosa hybrida* demonstrated that under continuous light conditions, plants showed a decrease in chlorophyll content (Table 3).

Additionally, chlorophyll levels remained relatively unchanged in plants of *Licopersicum esculentum* exposed to artificial light at night, despite the presence of yellowing and the initial phenomenon of patchy chlorosis [88]. The authors posited that the outcome was the result of a photoadaptation process of the tomato plants.

With regard to chlorophyll fluorescence, analyses related to artificial light and its effects are very few and fewer than all the other physiological parameters analyzed.

In general, exposure to artificial night light generated a significant alteration of parameters such as effective quantum yield, photochemical quenching, and electron transport rate (Table 2) in *Euonymus japonicus* [23] and other species such as *Saraca asoca*, *Terminalia catappa*, *Bauhinia variegata*, and *Holoptea integrifolia* [27]. Also in this case, plants exposed to light showed values dictated by a condition of overstimulation and activity of the plant photosynthetic system with harmful consequences to its physiology [6,23,24,27].

Prolonged exposure to artificial light has led, as shown in several studies mentioned below, to various criticalities in the normal dynamics of sugars: continuous nighttime exposure to artificial light can negatively affect their quantity and accumulation [32].

Artificial lighting can be described as a real threat to balance and the dynamics of sugars in plants because it interferes with the circadian clock and physiological processes such as photosynthesis. Leaves during the day cycle use light energy to fix CO_2 and produce sugar and starch that will be fundamental during the night cycle as a carbon sink to ensure the growth and normal metabolic functioning of plants [11]. These carbohydrates are accumulated during periods of intense photosynthesis in roots, stems, and shoots to maintain plant functionality [78,89–91].

The analysis of soluble sugar content showed that in six of the eight species, the soluble sugar content varied [32]. In four of the six species (*Tilia tomentosa*, *Acer campestre*, *Kerria japonica*, *Spiraea* x *cinerea*), sugar reduction was observed in the apical buds of both artificial light treatments compared to the control. Conversely, in the remaining two species (*Cornus alba*, *Lonicera pileata*), the L-LP group showed an increase in sugars, which was indicative of broader-spectrum physiological stress conditions.

In [11], the sugar analysis of two deciduous species was evaluated considering the three phenological stases of the leaves (young, mature, and senescent) at sunrise and at night. *Tilia tomentosa* exposed to artificial light accumulated less starch in young and mature leaves than the control did. In contrast, no significant differences in the quantity of starch were found in senescent leaves. A similar situation was found in the exposed poplar, except for the senescent leaves, which showed lower accumulated starch values in the control compared to the exposed plants. This would explain the delayed senescence and leaf loss processes compared to the control. Considering this, it is possible to state that the exposed plants of both species showed a lower ability to accumulate starch and a greater rate of starch degradation compared to control plants. As regards the soluble fraction of sugars in *Platanus* x *acerifolia* and *Tilia platyphyllos*, despite a greater degree of starch degradation, no statistically significant compensation values were found, indicating that the translocation of sugars from the leaves to the organs was effectively regulated.

In another study, which evaluated the impact of artificial light on the quantity of non-structural carbohydrates on *Euonymus japonicus* and *Rosa hybrida*, the soluble sugar and starch content in the plants exposed to artificial light were found to be greater than in not exposed plants [23]. This increase was likely due to an inhibitory effect on the enzymes responsible for their degradation, which may be caused by continuous exposure to light. This process can determine a phase shift in the dynamics and re-articulation of sugars in the plant metabolism, with consequent accumulation in the leaf organs [92]. This was also confirmed on *Oryza sativa* [93], a species that was subjected to light treatment with different intensities (Table 3). This study demonstrated that exposure to low-intensity light (2000 lux) at night modifies the activity of the enzyme α-amylase, consequently influencing the metabolism of sugars. α-Amylase plays a fundamental role in the development of cereal species, facilitating the breakdown of starch into soluble sugars. The stimulation of this enzyme by light determined a greater amount of soluble sugars compared to species not exposed to continuous light at night, thus confirming a negative interference in the metabolism of individuals.

An important broad-spectrum information contribution, taking into account the effect of ALAN on stomatal movements directly related to the endogenous regulation of abscisic acid, the synthesis and degradation of starch, and the structural conformation of chloroplasts, is reported in [65]. This study then interprets how the light signals from outside interact with the plant's internal responses.

Three-year research was carried out on one-year-old *Lirodendron tulipifera* in a greenhouse. The plants were divided on a treatment basis (Table 2), and analyses were carried out at sunset and sunrise. The plants exposed to treatments showed that there were reductions in the stomatal opening and a morphological difference in the type of opening, which was longer and narrower in the treated plants. The starch content of exposed plants was lower than that of control plants, probably due to inhibition of the same synthesis and structural alteration in chloroplasts from stressed plants. The inhibition in starch synthesis generated a cascade effect on the guard cells, which influenced the stomatal movement.

Also, abscisic acid is part of the signaling pathway involved in opening and closing stomata, and the plant biological clock also regulates it. This hormone was strongly reduced at sunset in the treated plants, whereas it was reduced at dawn in the control plants. Exposure to artificial light resulted, therefore, in a significant alteration of the abscisic acid at sunset and a slow degradation of the same hormone at dawn, compared to control plants. Based on these results, the treated plants showed a loss of turgor in the guard cells and an alteration of regulation in the daytime stomatal opening [65].

Table 3. Description of treatments and effects on gas exchange, leaf chlorophyll content chlorophyll fluorescence, and carbohydrate dynamics in response to different lamp types.

Type of Illumination	Species	Treatment and Set-Up	Effects	Reference
LED	*Tilia platyphillos*, *Platanus* x *acerifolia*	No treatment [CNT] ~700 µmol m^{-2} s^{-1} [−700] ~300 µmol m^{-2} s^{-1} [−300] Monthly analysis at night, dawn, and sunrise	Plants with both treatments showed significant differences in Pn compared to CNT—+36% of chlorophyll amount in treated *T. platiphyllos* and +15% of chlorophyll amount in treated *P. acerifolia* compared to CNT	[11]
LED	*Tilia tomentosa*, *Betula pendula*, *Fagus sylvatica*, *Acer campestre*, *Cornus alba*, *Lonicera pileata*, *Kerria japonica*, *Spiraea* x *cinerea*	C: shoots for 12 h at 100 mmol m^{-2} s^{-1} and for 12 h at 0 mmol m^{-2} s^{-1} M-LP: shoots for 12 h at 100 mmol m^{-2} s^{-1} and 12 h at 30 mmol m^{-2} s^{-1} of light. L-LP: shoots for 12 h at 100 mmol m^{-2} s^{-1} and 12 h at 1 mmol m^{-2} s^{-1}.	L-LP, M-LP: Six species showed varied soluble sugar content compared to the C	[32]

Table 3. *Cont.*

Type of Illumination	Species	Treatment and Set-Up	Effects	Reference
LED	*Tilia platyphillos*, *Platanus* x *acerifolia*	No treatment [CNT] ~700 µmol m^{-2} s^{-1} [−700] ~300 µmol m^{-2} s^{-1} [−300] Analysis of young, mature, and senescent stages of leaves	Ability to accumulate starch and a greater rate of starch degradation of treated plants of both species and treatments < CNT plants	[11]
LED	*Oryza sativa*	12 h of day + 12 h of darkness	Change in activity of the enzyme α-amylase	[93]
LED	*Euonymus japonicus*, *Rosa hybrida*	Plants exposed to LED controlled by a light-sensitive switch at night	Soluble sugar and starch content in plants exposed > not exposed plants	[23]
HPS	*Liriodendron tulipifera*	One years-old plants in greenhouse	Alteration of stomatal regulation, chloroplast structure, synthesis, and degradation of abscisic acid and starch	[65]
LED	*Cymbidium* sp.	Night treatments: 2 h (from 23:00 to 01:00), 4 h (from 22:00 to 02:00), 6 h (from 21:00 to 03:00), 8 h (from 20:00 to 04:00), 16 h (continuous light, from 17:00 to 9:00) −10, 100, 200 µmol·m^{-2}·s^{-1}	Decrease of SPAD value and activation of photosynthetic process at night	[87]
A mixture of cool-white fluorescent and incandescent lamps	*Arachis hypogea*	Growth-chamber and continuous light at canopy level 500 µmol^{-2} s^{-1} for 12/12-h light period and 250 µmol^{-2} s^{-1} for the 24-h light period	Reduction of Pn and gas exchange	[85]
LED	*Euonymus japonicus*, *Rosa hybrida*	Plants exposed to LED controlled by a light-sensitive switch at night	Significant reduction in the amount of chlorophyll and significant reduction of Pn, effective quantum yield and gs	[23]
HPS	*Licopersicum esculentum*	Plants transplanted into tomato and pepper peat bags in greenhouses and under natural light or with supplemental light of 120 µmol·m^{-2}·s^{-1} for 12–18–24-h.	No significant reduction in the amount of chlorophyll but the presence of the initial phenomenon of chlorosis	[88]
LED	*Saraca asoca*, *Terminalia catappa*, *Bauhinia variegata*, *Holoptelea integrifolia* *Thervetia peruviana*, *Ficus benjamina*	Trees in urban areas near LED lamps	Alteration of chlorophyll fluorescence and electron transport efficiency in deciduous plants	[27]

6. Conclusions

The studies here reviewed highlighted the multifaceted effects of artificial light on plants, offering insights and perspectives to guide future research in this evolving and stimulating field.

Artificial nighttime light can have significant detrimental effects on tree species. These effects span various phenological and physiological aspects impairing the plant's ability to thrive, especially in urban environments where the problem of artificial light at night is more severe. In terms of plant phenology, the effects of light exposure were similar across different experimental setups, i.e., controlled and field conditions; different types of lamps, i.e., HPS and LED; and across different phenological stages and species. Furthermore, the effect of ALAN on plant phenology in urban areas was enhanced when combined with other stressors. On the other hand, the results of the reviewed studies concerning the effect of ALAN on plant physiology were less consistent depending on the species and functional traits considered.

A key theme that emerged from the literature reviewed was the lack of information, particularly on the physiological effects of different lighting technologies and the effects of specific wavelengths of light. Nevertheless, it must be emphasized that a comparative analysis of the long-term impacts of HPS and LED lighting is probably no longer necessary, as the massive conversion to LED lamps in urban areas is increasingly widespread and the HPS phenomenon is destined to become extinct within a few years.

It is therefore advisable to pay more attention to LED lamps, to know their spectra and intensities, to have full awareness of which conditions are most harmful to plants in the city, and to study strategic plans for their installation. The ability of LED technology to dynamically adjust its spectral output also presents an opportunity to reduce the negative impacts of artificial light on plants, and research should explore how tunable spectra could be used to optimize urban lighting with minimal damage to plant physiology.

While the trend towards "smart" cities and energy-efficient lighting such as LED lamps is essential for reducing energy consumption and environmental damage, this review highlights the need to reconsider how artificial light interacts with urban vegetation. Urban greenery plays a crucial role in providing ecosystem services, thus making it imperative to monitor and mitigate the impacts of photopollution in urban environments. Given the multi-stress conditions that urban plants endure, it is of paramount importance to consider photopollution as a significant urban stress factor and to undertake targeted research into the species-specific responses to it. In particular, the adoption of experimental approaches that consider both controlled and field environments may facilitate a more detailed understanding of the complex dynamics between artificial light, heat, and drought stressors.

This knowledge will guide the selection of species that are most resilient to urban conditions and aid in optimizing green spaces in smart city planning. Urban planners, ecologists, and policymakers should collaborate to reassess lighting designs and urban planting schemes. Such efforts will not only improve the resilience of urban plant life but also enhance the broader ecological and social benefits of urban greenery.

To gain insight into the broader implications of artificial lighting on plant physiology, it is also imperative to analyze the effects of ALAN on circadian rhythms. Although it is well documented that ALAN disrupts the circadian rhythms of plants, there is still a paucity of studies that examine the relationship between the alteration of specific functions induced by the alteration of circadian rhythms induced by ALAN and physiological performance in terms of ecophysiological traits related to gas exchange.

Another area of uncertainty lies in the variability of plant responses between species. Many photopollution studies generalize their findings across plant species, but significant interspecies variation is likely to exist. The long-term impacts of chronic exposure to artificial light have been poorly studied. The effects of prolonged exposure, particularly over multiple growing seasons, on plant health and interactions with other organisms such as pollinators and herbivores are not well understood.

Moreover, another point to take into consideration is the imbalance of information that we have on deciduous species to the detriment of evergreen ones. The latter are little investigated in the works present in the literature on the effects of artificial light, and this lack is still notable, particularly based on the presence and quantity of individuals of evergreen plants, for example, in the Mediterranean basin. This gap must therefore be filled with targeted studies that also investigate the same parameters for species such as *Quercus ilex*, *Viburnum tinus*, *Nerium oleander*, and others that are very widespread in Mediterranean cities.

The interaction between photopollution and other environmental stressors, such as temperature fluctuations, drought, and air pollution, also needs to be further expanded. The association between artificial light stress and heat stress in urban areas could be an excellent advancement of knowledge in this sense.

ALAN represents an increasingly significant environmental challenge with the potential to engender far-reaching ecological consequences, including impacts on biodiversity and ecosystem dynamics. By acknowledging and addressing the impact of light pollution on plant biology through a multi-scale approach, it will be possible to achieve a more balanced approach to the use of night-time illumination in urban areas, while ensuring the preservation of ecological integrity.

Author Contributions: Conceptualization, L.F. and L.V.; methodology, L.F and L.V.; writing—original draft preparation, L.F.; supervision, L.V. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4-Call for tender No. 3138 of 16 December 2021, rectified by Decree n.3175 of 18 December 2021 of Italian Ministry of University and Research funded by the European Union-NextGenerationEU. Award Number: Project code CN_00000033, Concession Decree No. 1034 of 17 June 2022 adopted by the Italian Ministry of University and Research, CUP B83C22002950007, Project title "National Biodiversity Future Center-NBFC".

Data Availability Statement: The data will be made available by the authors on request.

Conflicts of Interest: The authors declare no conflicts of interest.

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