

FUTURE DIRECTIONS

Ecological effects of artificial light at night on wild plants

Jonathan Bennie*, Thomas W. Davies, David Cruse and Kevin J. Gaston

Environment and Sustainability Institute, University of Exeter, Penryn Campus, Penryn TR10 9FE, UK

Summary

1. Plants use light as a source of both energy and information. Plant physiological responses to light, and interactions between plants and animals (such as herbivory and pollination), have evolved under a more or less stable regime of 24-h cycles of light and darkness, and, outside of the tropics, seasonal variation in day length.

2. The rapid spread of outdoor electric lighting across the globe over the past century has caused an unprecedented disruption to these natural light cycles. Artificial light is widespread in the environment, varying in intensity by several orders of magnitude from faint skyglow reflected from distant cities to direct illumination of urban and suburban vegetation.

3. In many cases, artificial light in the night-time environment is sufficiently bright to induce a physiological response in plants, affecting their phenology, growth form and resource allocation. The physiology, behaviour and ecology of herbivores and pollinators are also likely to be impacted by artificial light. Thus, understanding the ecological consequences of artificial light at night is critical to determine the full impact of human activity on ecosystems.

4. *Synthesis.* Understanding the impacts of artificial night-time light on wild plants and natural vegetation requires linking the knowledge gained from over a century of experimental research on the impacts of light on plants in the laboratory and glasshouse with knowledge of the intensity, spatial distribution, spectral composition and timing of light in the night-time environment. To understand fully the extent of these impacts requires conceptual models that can (i) characterize the highly heterogeneous nature of the night-time light environment at a scale relevant to plant physiology; and (ii) scale physiological responses to predict impacts at the level of the whole plant, population, community and ecosystem.

Key-words: circadian, ecophysiology, light cycles, light pollution, photoperiodism, photopollution, physiology, sky glow, urban ecology

Introduction

Light plays a central role in the physiology and ecology of plants. Plants use light both as a resource, via photosynthesis, and as a source of information. The timing, intensity and spectral composition of natural cycles of light provide cues for regulating circadian rhythms, seasonal phenology and the expression of phenotypic variation, including growth form and resource allocation. These cycles have provided a strong selective pressure for millennia. Since the early 20th century, the widespread use of outdoor electric lighting associated with human settlements, industry and transport networks has altered these natural daily and seasonal cycles of light across much of the globe (Cinzano, Falchi & Elvidge 2001), not just

in urban environments but also in natural ecosystems (Bennie *et al.* 2015a; Gaston, Duffy & Bennie 2015). Meanwhile, there is an increasing recognition of the value of frequently illuminated habitats such as roadside verges and hedgerows (Tikka, Högmänder & Koski 2001; Hovd & Skogen 2005; Cousins 2006; Le Viol *et al.* 2008; Hanley & Wilkins 2015), domestic gardens (Davies *et al.* 2009; Goddard, Dougill & Benton 2010) and urban ecosystems (Angold *et al.* 2006) for plant and pollinator biodiversity and maintenance of ecosystem services, including human health and well-being (Gaston, Ávila-Jiménez & Edmondson 2013). It has been estimated that 238 000 hectares of road verge alone exist in Britain, more than twice the area of natural or semi-natural grassland in the wider countryside (Plantlife 2013). These habitats are often directly illuminated by artificial light throughout the night, or intermittently lit by vehicle headlights. However,

*Correspondence author. E-mail: j.j.bennie@exeter.ac.uk

even reviews of the ecological effects of roads seldom give much attention to artificial light at night (Spellerberg 1998; Trombulak & Frissell 2000; Coffin 2007; although see Blackwell, DeVault & Seamans 2015). Many other natural or semi-natural habitats may be directly lit from artificial light sources at their margins when they are adjacent to human settlements, industry or roads. Even remote areas may be affected as measurable levels of artificial light reflected and scattered in the atmosphere ('skyglow') are detectable tens to hundreds of kilometres from urban centres, particularly under overcast conditions (Kyba *et al.* 2015). Cinzano, Falchi & Elvidge (2001) concluded that 'mankind is proceeding to envelop itself in a luminous fog', after calculating that some 18.7% of the World's terrestrial surface (excluding Antarctica) could be considered as experiencing light pollution. This figure is far higher for some countries – 84.7% of the United Kingdom, for example, or 100% of the Netherlands.

Some measurable degree of artificial light at night is clearly the norm, rather than an exception, across the land surface of many developed countries, but such figures mask a high degree of spatial heterogeneity; while the scattered light from a city may illuminate natural vegetation to levels approaching that of moonlight, localized direct illumination from vehicle headlights or roadside street lighting will be several orders of magnitude brighter. Many natural or semi-natural habitats thus experience artificial light at night at levels congruent with those that cause physiological effects on plants. There is an extensive literature on the effects of artificial manipulations of light conditions on plants, dating from the 17th and 18th centuries (Hunt 1854; Darwin 1881), and it is well-established that light at night, even of short duration or at low intensities, can have marked physiological effects (Smith 1982). Surprisingly, despite a growing awareness of the impacts that disruption of natural light cycles may have on animals (Longcore & Rich 2004; Gaston & Bennie 2014) and plant–animal interactions (MacGregor *et al.* 2014), much less work has been published on the unintended ecological impacts of artificial light at night on wild plants and natural vegetation (although see Briggs 2006 for a review of potential physiological mechanisms). In this study, we argue that there is a pressing need for plant ecologists to define ecologically meaningful measures of artificial light in the natural environment and to develop understanding of the thresholds and dose–response relationships of light-sensitive processes in plants, particularly at low light intensities. Furthermore, we must improve understanding of the effects of low-intensity light at night in terms of ecological, as well as physiological, processes including competition, herbivory, pollination, reproduction and dispersal.

How much artificial light is there in the environment?

Understanding the ecological impacts of artificial light requires information on the intensity, spatial pattern, spectral distribution, duration and timing of the artificial light to which wild plants are exposed. This is not straightforward, as any comparison of light levels in the environment is somewhat

complicated by high degrees of temporal and spatial heterogeneity, and the wide range of spectral power distributions of lighting systems in use (Gaston *et al.* 2012). Furthermore, there is no single measure of light intensity that is suitable for quantifying the varying physiological effects of artificial light on plants. In physical studies, the intensity of solar energy on a surface (solar irradiance) is typically measured as an energy flux density with SI units of W m^{-2} . These radiometric units, which measure power from the electromagnetic spectrum (including light), are distinct from photometric units, which describe the measurement of light in terms of its perceived brightness. Hence, the visible light flux on a surface is described in terms of illuminance, rather than radiance, as not all wavelengths are visible to the human eye. In order to convert measures of irradiance to illuminance, the energy flux must be weighted by a luminosity function, which describes the sensitivity of human visual perception to different wavelengths of light between 400 and 700 nm (Sharpe *et al.* 2005). The SI unit of illuminance is lux (lx), equal to one lumen (lm) per metre squared, where a lumen is the unit of luminous flux, which is the amount of visible light emitted by a source.

Figure 1 shows a range of illuminances measured in vegetation the UK. At the upper end of the scale, the leaves of trees adjacent to street lights or in the beam of car headlights may be exposed to thousands of lux while typical stable ground level illuminances of roadside vegetation (directly beneath street lights) are around 50 lux. Skyglow within cities has been recorded at levels of 0.1–0.5 lux (Eisenbeis 2006), and decreases with distance from central urban areas, with detectable levels up to 10s to 100s of km (Biggs *et al.* 2012).

Undesirable light at night, or light pollution, is often measured in other units. To measure the brightness of the night sky (including skyglow), astronomers often use the logarithmic magnitude scale, which was developed to compare the apparent brightness of stars; for example, Sirius, the brightest star in the sky, has magnitude -1.5 which is equivalent to an illuminance of 10^{-5} lx. When used to describe the brightness of the sky due to light pollution, measurements are typically taken vertically for a small portion of the sky (Davies *et al.* 2013; Kyba *et al.* 2015) and expressed as brightness per solid angle of the sky dome (magnitude per square arcsecond). A direct conversion into a measure of illuminance is problematic, however, since skyglow is strongly anisotropic, usually much brighter towards the horizon in the vicinity of towns and cities.

While radiometric measurements are essential for calculations of the energy balance of a surface, and photometric measures are useful for assessing the relative brightness of light to the human eye, in isolation neither is an ideal measure for assessing the ecological impact of light, particularly where that light derives from sources with a range of different spectral signatures. In this study, we use photometric units such as lux (lx) as a standard unit of comparison for light measurements – this has the advantage of allowing a direct comparison to levels of illuminance required for human activity. However, we stress that illuminance is only useful as a

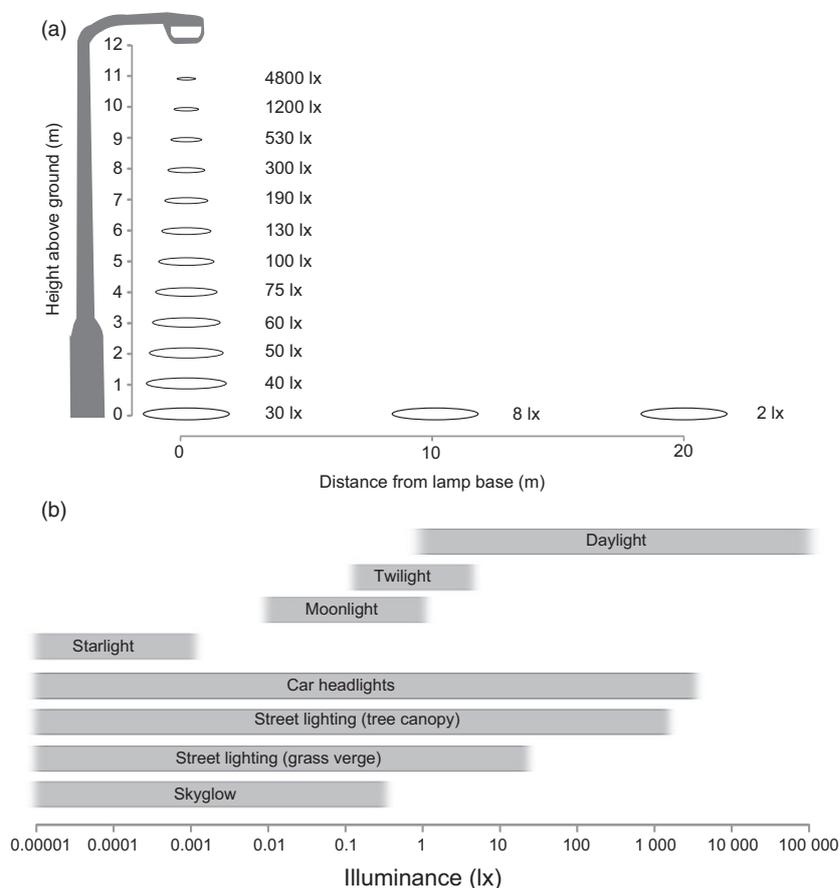


Fig. 1. (a) illuminance measured in the horizontal plane from a typical street light (Phillips Cosmopolis, metal halide lamp). The intensity of light decays rapidly with distance to the lamp. (b) comparison of measured illuminance from natural sources of light to artificial light sources – axis is on a logarithmic scale, and bars present approximate ranges based on field measurements.

proxy for the biological effects of light when information on the spectral power distribution of light, and the action spectra of the response, is also available. In ecological studies, the physiological pathway, and hence the spectral sensitivity of the photoreceptors involved, will often be unknown. Wherever possible, sample spectra and/or descriptions of the type of light source should be provided.

Correlated colour temperature (CCT) is frequently used as a description of spectral power distribution for vision-lighting systems. The CCT of a light source is the temperature (K) of an ideal blackbody radiator that radiates light of a comparable hue to the source. As a description of the spectral power distribution, and hence the biological effects, of a light source CCT is only meaningful when the source approximates a blackbody, as is the case with the sun, flames or incandescent bulbs. For other light sources, CCT gives an approximation of the aesthetic appearance of white light (from ‘cool’ blue lights to ‘warm’ orange), but is a poor indicator of the spectrally dependent response of photoreceptors.

A final factor to consider when measuring light in ecological studies is the orientation, field of view and angular response of the sensor, compared to the geometry of light-sensitive plant organs. Typically, light sensors have a field of view approaching 180° and are cosine corrected, so that the measured flux approximates that on a planar surface; commonly they will be mounted *in situ* horizontally, effectively measuring the flux on a horizontal plane. In this case, light

sources positioned horizontally from the sensor, for example at or near the horizon, will make a small contribution to the measured flux. This is appropriate for a flat surface such as a leaf parallel to the sensor plane. However, interception of light by the organs of a plant may occur at a range of angles, including horizontally. Depending on the nature of the process, incident light fluxes on a horizontal plane, light on a vertical plane or integrated flux on the surface of a sphere may be more appropriate.

How do plants sense light?

Since the 19th century, it has been known that a plant’s response to light can be sensitive to wavelength. Hunt (1844, 1854) identified that the extreme red portion of the spectrum was associated with flowering and that blue light induced germination of seed, independently of the broad spectral range of light associated with the ‘decomposition of carbonic acid’ (photosynthesis). During the 20th century, several plant pigments involved in these and other responses were identified, and action spectra for several such photoreceptor pigments have been defined; for example cryptochrome has been shown to respond to light between 390 to 530 nm (violet to blue/green; Ahmad *et al.* 2002); phototropins respond primarily to blue light (Christie 2007); and phytochrome primarily to red and/or far-red light, depending on the form (Casal, Candia & Sellaro 2014). In algae, a wide range of pigments spanning

the visible spectrum have been identified (Rockwell *et al.* 2014).

The best known action spectrum for plants is that of photosynthesis; photosynthetically active radiation (PAR), usually defined as light between 400 and 700 nm, has an action spectrum defined by the absorbance spectra of chlorophyll and carotenoids. Because photosynthesis is a quantum process, the flux of photons, rather than energy is appropriate, and it is usually quantified as a photosynthetic photon flux density (PPFD) with units of $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. As short-wavelength photons carry more energy than those at longer wavelengths, and both the sensitivity of human vision and that of photosynthetic pigments vary considerably in their absorption at different wavelengths, the relationship between irradiance, illuminance and PPFD is strongly sensitive to the spectral distribution of the light source. The effect of artificial light at night on net photosynthesis in the environment is limited due to the low quantum flux densities associated with outdoor lighting when compared to daylight. While theoretically urban skyglow may be sufficient to induce a small photosynthetic response (Raven & Cockell 2006), in practice measurable effects on carbon fixation are likely to be limited to situations where leaves are in very close proximity to light sources (such as the canopies of trees around street lights), or when artificial lighting is introduced into naturally dark situations such as cave systems. In the latter case, the installation of lighting in caves for tourism is often sufficient to support *Lampenflora*, communities of algae, bryophytes and vascular plants solely reliant on electric lighting as an energy source (Lefèvre 1974; Johnson 1979).

In addition to the use of light as an energy source for photosynthesis, plants utilize a suite of other photoreceptors in order to sense information about their environment, the time of day and season of the year. The photosynthetic system itself is sensitive to light at night, providing a set of secondary pathways through which artificial light could influence carbon fixation. Poulin *et al.* (2014) showed that low levels of light from a high-pressure sodium street light, at an illuminance equivalent to that observed at the shore of an urban lakeside (6.6 lux), significantly changed several aspects of the photobiology of phytoplankton, including decreasing the intracellular chlorophyll *a* concentration and the number of Rubisco molecules per cell. In higher plants, light quality, even at low fluence rates, is known to affect physical characteristics of the photosystem, such as leaf stomatal density, as well as the opening of stomata (Smith 1982).

Many photoreceptors have been identified, of which three main groups have been characterized – phytochromes, cryptochromes and phototropins. Phytochromes, of which phyA and phyB play the dominant roles, are present in plants in two forms, P_r and P_{fr} . The P_r form absorbs light following an absorption spectrum with a peak sensitivity at a wavelength of around 650–670 nm, in the red portion of the spectrum; on absorbing light, a molecule in the P_r form converts into the P_{fr} form. The P_{fr} form has a different absorption spectrum, lacking such a distinct red peak but with another peak in the far-red, at 705–740 nm. On subsequently absorbing light (or

in darkness), the P_{fr} form is converted back to P_r . Each phytochrome molecule thus acts as a ‘switch’, flipped from one form to another by different wavelengths of light. Any light source can be characterized by a ‘phytochrome stationary state’ (PSS; Sager & McFarlane 1997), an estimate of the relative proportion of far-red absorbing (P_{fr}) to total ($P_r + P_{fr}$) phytochrome within tissues at equilibrium under a stable light source, calculated from the phytochrome cross-sectional area for each form and the spectral irradiance of the light source. Since daylight beneath the shade of a photosynthetic canopy is depleted in red light relative to far-red (Franklin & Whitelam 2005), the PSS is an indication of the degree of shading by other plants that a plant is experiencing. Phytochrome is also used to detect photoperiod and hence plays an important role in the initiation of phenological events such as budburst, flowering and senescence. Flowering plants are often characterized as falling into one of three groups – short-day plants, in which flowering is initiated, advanced or promoted when a dark night-time period is sufficiently long to allow enough phytochrome in the P_{fr} form to revert to P_r ; long-day plants, in which the dark night-time period must be sufficiently short to increase the night-time levels of P_r ; and day-neutral plants which have no detectable effect of darkness on their flowering phenology, but rely on other environmental cues. The detection of photoperiod in plants can be very sensitive – Rivera & Borchert (2001) provide evidence that in the tropics, where annual variation in day length is less than one hour, photoperiodism is still used as a seasonal cue for flowering in some tropical trees. Early experimental work showed that even brief exposure to red light at night can be sufficient effectively to interrupt the detection of an unbroken dark period, and prevent flowering in short-day plants, while subsequent exposure to far-red light can reverse the effects of the interruption (Borthwick *et al.* 1952). Intermittent light of certain wavelengths may thus be effective in shortening the perceived day length – indeed, cycling pulses of lights for just six minutes every half hour can be as effective as continuous light (Runkle *et al.* 1998; Blanchard & Runkle 2010). Low levels of lights are often effective in inducing a response. Whitman *et al.* (1998) found that effects on flowering saturated at levels as low as < 0.05 and $0.4 \text{ mol m}^{-2} \text{ s}^{-1}$ PPFD from a broad-spectrum white light source, roughly equivalent to < 3.5 –28 lux, and well within levels recorded in roadside vegetation. By contrast, Ishikawa *et al.* (2009) found a fluence-dosage response in rice in which the degree to which flowering was suppressed increased with the light intensity supplied.

Detection of photoperiod in plants is not always, if ever, a simple function of the photoreversible forms of phytochrome, however. In the facultative long-day plant *Arabidopsis thaliana*, night interruptions from red, far-red or blue light are all effective in inducing flowering (Goto, Kumagai & Koornneef 1991). Cryptochromes, sensitive to light in the UV-A, violet and blue portions of the spectrum, act together with phytochromes to regulate the circadian clock, keeping daily rhythms set to a 24-h cycle of light and darkness. Photoperiodic control of flowering integrates both the circadian clock, and sensing of the length of the dark period; thus, there is an

interaction between the detection of daily and seasonal cycles, and between photoreceptor systems. The cryptochrome/photolyase family of photoreceptors also plays critical roles in controlling a wide range of light-induced responses in germination, growth and development, and shade avoidance (Kami *et al.* 2010), as well as DNA repair (Fortunato *et al.* 2015). A further blue light-sensitive receptor protein, phototropin, is responsible for phototropism, the growth of plant organs towards a light source.

Figure 3 shows the spectral power distribution of five types of lighting frequently used in outdoor street lighting, along with the relationship between PPFD (photosynthesis), the PSS (phytochrome) and the relative amount of blue light between 350 and 500 nm (cryptochrome and phototropins).

The detection of light in plants is complex, often relies on more than one physiological pathway and may have partial redundancy, so that processes induced by one photoreceptor system may also be induced or repressed by another system (Song, Ito & Imazuimi 2010). Furthermore, processes that rely on light-induced responses such as photoperiodism in one species or phenotype may be linked to other environmental cues in others (Basler & Körner 2012).

How do plants respond to artificial light at night?

DIRECT EFFECTS

With the exception of a handful of original papers and the review of Briggs (2006), surprisingly few studies apply knowledge of the physiological effects of light on plants to examining the effects of exposure to artificial light in the environment. This is particularly surprising as experimental

studies have shown that relatively low levels of light (Whitman *et al.* 1998) or light over a short duration (Runkle *et al.* 1998) can be effective in influencing the response of plants to photoperiod – such levels are frequently observed under conditions of night-time lighting in the environment (Figs 1 and 2). Furthermore, the high red to far-red ratio of most common forms of outdoor lighting compared to sunlight make them particularly effective in disrupting detection of photoperiod through the phytochrome pathway, while blue-rich LED lighting, which is rapidly being adopted in many regions, emits strongly in the region of the spectrum to which cryptochrome and phototropins are sensitive (Fig. 3). In the context of light pollution, these observations suggest several key areas for research, namely – How widespread are ecologically significant physiological effects of artificial light on plants in the environment? What is the relative contribution of ambient low-level light (e.g. skyglow), continuous direct illumination (e.g. street lighting) and intermittent pulsed light (e.g. vehicle headlights)? And can ecological impacts be mitigated by selecting light sources with specific spectral characteristics?

Some of the earliest documented effects of artificial light at night on plants in urban environments concerned the retention of leaves on deciduous trees in the vicinity of street lights (Matzke 1936). Certain tree species appear to be more sensitive to direct illumination than others, but it is a common phenomena in several species planted as urban roadside trees. In North America, this phenomenon has been recorded in *Populus canadensis*, *Salix fragilis* (Matzke 1936), *Populus nigra*, *Ulmus americana* (Schroeder 1945) and *Liquidambar styraciflua* (Briggs 2006). In both Europe and North America, it is widely observed in *Platanus* species (Matzke 1936; Schroeder 1945; Briggs 2006; Fig. 4), and in Europe, it has been observed in *Aesculus hippocastanum* and *Betula pendula*

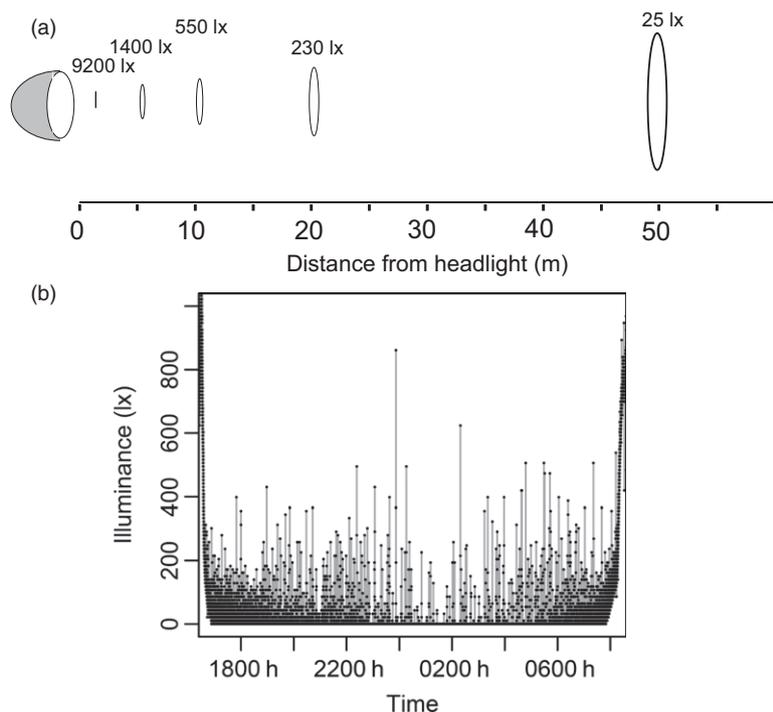


Fig. 2. Illuminance from car headlights. (a) Measured light at set distances in front of a vehicle (2013 Vauxhall Astra) with high intensity discharge (HID) headlights. (b) variation in illuminance measured in roadside vegetation between sunset and sunrise on a rural main road with no fixed lighting. Peaks represent pulses of light from passing vehicles. Typically, light from these sources has a high degree of variability, but can reach much higher magnitudes than those under street lights (see Fig. 1).

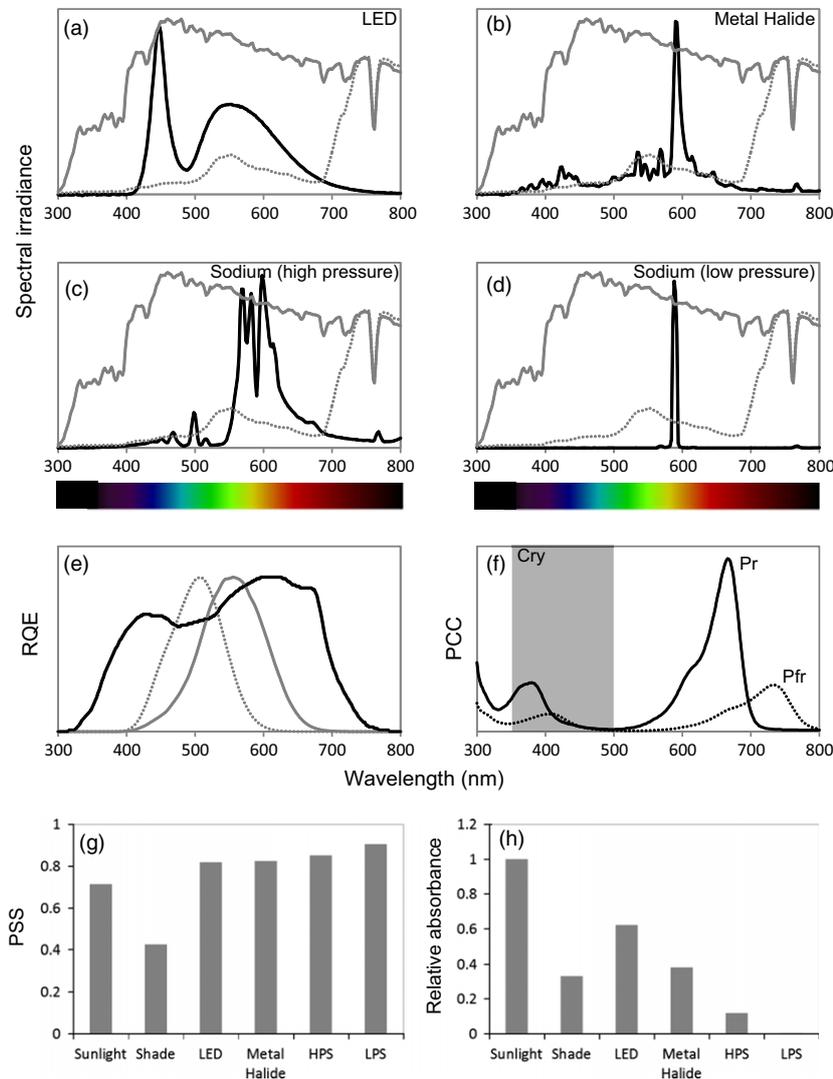


Fig. 3. (a–d) black lines show the measured spectral irradiances of four contrasting types of street lights currently used on roads in Cornwall, UK; ‘white’ LED, metal halide, high-pressure sodium and low-pressure sodium. For comparison the grey line shows a measured spectral irradiance of daylight on a cloudy day; the dashed grey line shows the irradiance under a dense canopy of leaves on the same day. (e, f) show standardized biological spectral response functions; in e the black line represents the relative quantum efficiency (RQE) of photosynthesis, the grey lines show a standard luminosity function for human photopic (solid line) and scotopic (dashed line) vision (CIE 1951; Sharpe *et al.* 2005), representing the sensitivity of the human eye to light under normal and low-light conditions. In (f) the black lines represent the photochemical cross-sectional area of two forms of phytochrome Pr (solid line) and Pfr (dashed line). The grey shaded area (Cry) represents the approximate region of the spectrum to which cryptochrome is sensitive. (g, h) estimate the comparative impact of the four light sources on plant photoreceptors; (g) shows the phytochrome photostationary state (PSS), a measure of the equilibrium ratio of phytochrome in its Pr and Pfr forms under constant illumination from each light source; (h) shows the relative quantum count of light within the cryptochrome-sensitive region per unit illuminance, standardized so that the value for sunlight equals 1.

(Sybille Schroer, pers. obs.). Artificial light may also have a measurable effect on spring budburst in urban trees; at the University of Exeter’s Cornwall Campus, near Falmouth, U.K., budburst occurred up to two weeks earlier on branches of large-leaved lime trees in the vicinity of LED lighting (Fig. 5). In New Zealand, *Metrosideros excelsa* flowers more profusely next to street lights than between them (Jacqueline Beggs, pers. obs.) While such dramatic effects on budburst, flowering and leaf colouring and abscission are frequently observed in urban trees under direct illumination, very few scientific studies have described this phenomenon, and the effects on tree species that are rarely found in urban situations, and under lower levels of diffuse ambient light and on herbaceous species with less obvious phenological stages are poorly known. While these phenomena have been described predominantly in temperate trees, in seasonal tropical environments, budburst in trees may respond to changes in day length of 30 min or less (Rivera & Borchert 2001) and could be highly sensitive to artificial light at dawn and dusk.

Such changes in leaf and flowering phenology may have significant effects on the health, survival and reproduction of

plants. Matzke (1936) reported injury from low temperatures in leaves retained on urban trees under street lights. The timing of budburst and leaf fall of deciduous trees determines the exposure to frost damage of photosynthetic tissue (Hanninen 1991; Cannell 1997); it may also determine the exposure to fungal pathogens in spring (Marçais, Kavkova & Desprez-Loustau 2009) and to herbivores which time their emergence or activity to the emergence of leaves (Visser & Holleman 2001). The timing of budburst is often determined by interactions between temperature (both spring warmth and winter chilling) and photoperiod. Photoperiod is thought to be critical in late-successional species, which tend to trigger budburst later in the spring than early-successional species, which are triggered predominantly by temperature and insensitive to photoperiod (Basler & Körner 2012; Körner & Basler 2010).

Cathey & Campbell (1975a,b) found that a wide variety of ornamental garden plants were sensitive to artificial light at night, testing a variety of different light types and inducing marked effects on flowering and growth rates at illuminance levels comparable to those at which garden plants are frequently exposed (< 5 lux). Both suppression and induction of



Fig. 4. Retention of leaves into winter on deciduous trees in the vicinity of street lighting. The images show a London plane (*Platanus x acerifolia*) tree in Liverpool city centre on three dates in 2014. The entire tree is illuminated by artificial light, but the right hand side receives direct illumination from street lighting. Autumn coloration had not taken place and the most brightly lit portion of the crown retained leaves well into December. Photo: Steven Rawlings.

flowering, and enhanced and suppressed growth, were found, depending on species, and the response was greatest under light sources with a high proportion of red light and a high red/far-red ratio (such as high-pressure sodium lighting). Effects of light pollution on agricultural crops have also been reported, although little scientific work has addressed the issue; Briggs (2006) reports that bright floodlights from an Ohio prison prevented normal development of *Glycine max* (soya beans) in nearby fields, and Sinnadurai (1981) reported that *Zea mays* (maize) crops alongside main roads in Accra, Ghana, grew rapidly but failed to flower after high-pressure sodium lamps were installed. Less obvious effects in wild species may go unnoticed – in an experimental system, we have found that *Lotus pedunculatus*, a species in which flowering is known to be sensitive to day length (Forde & Thomas 1966), produced between 10 and 25% fewer flower heads under night-time artificial light treatments simulating street lighting (Bennie *et al.* 2015b).

DARK RECOVERY FROM STRESS

A period of darkness can be crucial for repair and recovery from environmental stresses. Tropospheric ozone is a major

global pollutant produced by photochemical reactions of precursors (nitrogen oxides and hydrocarbons) associated with road traffic (Munir, Chen & Ropkins 2012). Tropospheric ozone can have severe effects on vegetation (Ashmore 2005), including foliar injury. Plants at northern latitudes often display more signs of foliar injury, a phenomenon attributed to long day lengths impairing repair and defence processes (Vollsnes *et al.* 2009). Experimental studies have shown that constant artificial light at night at levels reported at approximately $1 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD (using a fluorescent lamp, equivalent to around 74 lux and within the range of exposure of roadside vegetation under street lighting; Fig. 1) significantly increased foliar injury due to ozone in three clover species (Futsaether *et al.*, 2009). This process is probably regulated by the phytochrome pathway as it can be induced by short periods of exposure to red light during the night (5–30 min) and reversed by subsequent exposure to far-red light (Eriksen *et al.* 2012). The combined effects of ozone damage and night-time illumination (including constant illumination from street lights or short bursts and high-intensity light from vehicle headlights) on vegetation near roads have not been studied.

PLANT–ANIMAL INTERACTIONS

In addition to direct effects on plants, artificial light at night is likely to influence interactions between plants and animals, potentially in complex ways. For example, light has been shown to affect caterpillars of the moth *Mamestra brassicae* by decreasing both male caterpillar and pupal mass and reducing the duration of pupation in both sexes (van Geffen *et al.*, 2014), as well as reducing activity and mating in *Operphtera brumata* (van Geffen *et al.* 2015). Winter moths are important herbivores of deciduous trees, causing defoliation in severe outbreaks (Wesołowski & Rowiński 2006). They typically show strong synchrony in egg hatching with spring budburst in host trees such as *Quercus robur*, but environmental change may disrupt this synchrony, leading to mismatches in timing between the insect and its host (Visser & Holleman 2001; Van Asch *et al.* 2007). Such mismatches in phenology are likely to occur when species respond individually to temperature and photoperiod. Disruption of seasonal light cues by artificial light, population level changes or aggregation of individuals could modify interactions including herbivory, pollination and seed dispersal. Both top-down and bottom-up effects are possible, although few studies have explicitly looked for evidence of such effects; in an experimental system, artificial light suppressed flowering in the legume *Lotus pedunculatus*, apparently leading to a subsequent suppression in numbers of the aphid *Acyrtosiphon pisum* feeding on flowering shoots (Bennie *et al.* 2015b). Street lighting can cause local aggregations of predatory invertebrates (Davies, Bennie & Gaston 2012), but the subsequent effects on herbivorous invertebrates and on plant species are unknown.

Many plant species rely on nocturnal or crepuscular pollinators and are adapted to some extent for night-flying flower

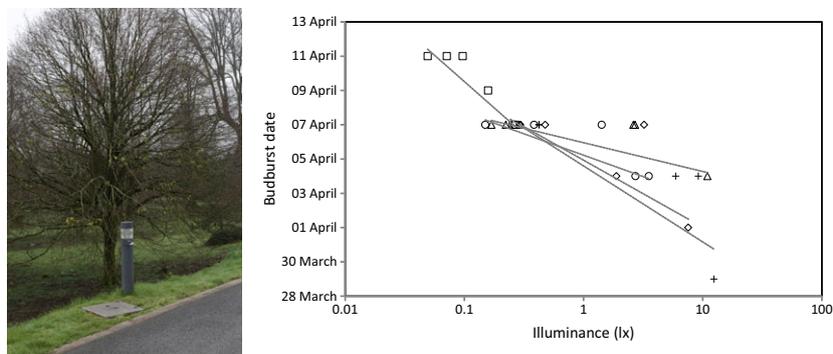


Fig. 5. Leaf out date (recorded when 50% or more of the buds nearest the apex have fully unfolded leaves) of five shoots from each of five mature small-leaved lime *Tilia cordata* trees adjacent to a footpath lit by white LED lighting on the university of Exeter's Penryn Campus in 2014 (one tree and lighting fixture illustrated on 1st April). Night-time illuminance levels were measured at each shoot on an overcast night at new moon prior to leaf unfolding. Each tree is represented by a different symbol, dashed lines represent regression lines for each individual tree, solid line represents overall regression line (significant at $P < 0.01$ with tree as a random effect). Photo: James Duffy.

visitors (Baker 1961). Macgregor *et al.* (2014) review the potential effects of light pollution on pollination by nocturnal Lepidoptera, a group that are strongly attracted to artificial light (Eisenbeis 2006; van Langevelde *et al.* 2011; Warrant & Dacke 2011). The effects are potentially complex – light may affect Lepidoptera at the population level through effects on reproduction and mortality and modify their phenology, as well as by modifying behaviour. Where ‘flight-to-light’ behaviour occurs, and insect pollinators are attracted to light, it is unclear at present to what extent lit vegetation will have a higher concentration of active pollinators, or whether the presence of light will act as an ecological trap or have a disruptive effect, reducing pollination rates (Eisenbeis 2006; Macgregor *et al.* 2014). In tropical and subtropical regions, bats may be significant pollinators of certain groups of flowering plants and of particular importance in long-distance pollen dispersal (Fleming, Geiselman & Kress 2009), as well as being important in seed dispersal (Fleming & Heithaus 1981). Light can act as a barrier to movement for many species of bats (Stone, Jones & Harris 2009, 2012), effectively fragmenting landscapes and potentially acting as a barrier for gene flow or dispersal in plants (Lewanzik & Voigt 2014). Effects on pollination may not be limited to nocturnally pollinated plants – artificial light may disrupt the behaviour and demography of diurnal as well as nocturnal animals, and habitats around roads are increasingly recognized as key habitats for pollinators (Hanley & Wilkins 2015).

Summary

The effects of artificial light at night on wild plants and natural or semi-natural ecosystems are of potential ecological significance world-wide. However, since the review of potential physiological mechanisms by Briggs (2006), surprisingly little research has been published on the impacts of artificial light in the as an environmental pressure for plants. There is relatively little information available concerning how pervasive are the ecological impacts of artificial light at night, the relative contributions of diffuse, direct, constant or intermittent

light sources and how any adverse effects may be mitigated. We suggest that plant ecologists should address this gap in knowledge by focusing on four key issues. First, the night-time light environment of plants in urban, suburban and natural ecosystems needs to be better characterized. Plants are exposed to extremely high degrees of heterogeneity in terms of the intensity, spectral power, timing and duration of light to which they are exposed, which complicates our understanding of how widespread ecological effects may be. Secondly, our understanding of the physiological effects of light need to be expanded into an understanding of the ecological effects, and we should search for population and community-level impacts as well as impacts at the individual level. Thirdly, interactions between direct and indirect effects of artificial light, for example those mediated through herbivores, pollinators, pathogens or competitors, should be explored. Fourth, there is a need to put studies of the effects of artificial light into the context of other stressors such as eutrophication, climate change, invasive species, chemical pollution, habitat fragmentation and invasive species. Artificial light will rarely affect wild plants in isolation, and there is a need not only to understand the relative importance of light pollution among other anthropogenic drivers of change, but also to investigate the combined impact of multiple stressors; roadside vegetation, for example, may act as a corridor for the dispersal of non-native species (Tyser & Worley 1992) and will be exposed to chemical pollution such as tropospheric ozone in addition to being exposed to artificial light. There is considerable potential for making progress in understanding the impacts of this increasing, but poorly understood environmental pressure.

Acknowledgements

We are grateful to two anonymous referees for their comments and suggestions for revision to this manuscript. The research leading to this paper was funded by the European Research council under the European Union's Seventh Framework programme (FP7/2007-2013)/ERC grant agreement no. 268504 to K.J.G. We are very grateful to Steven Rawlings and James Duffy for supplying photographs for the figures.

Data accessibility

This manuscript does not use data.

References

- Ahmad, M., Grancher, N., Heil, M., Black, R.C., Giovani, B., Galland, P. & Lardemer, D. (2002) Action spectra for cryptochrome-dependent hypocotyl growth inhibition in *Arabidopsis*. *Plant Physiology*, **2**, 774–785.
- Angold, P.G., Sadler, J.P., Hill, M.O., Pullin, A., Rushton, S., Austin, K., Small, E., Wood, B., Wadsworth, R., Sanderson, R. & Thompson, K. (2006) Biodiversity in urban habitat patches. *Science of the Total Environment*, **360**, 196–204.
- Ashmore, M.R. (2005) Assessing the future global impacts of ozone on vegetation. *Plant, Cell and Environment*, **28**, 949–964.
- Baker, H.G. (1961) The adaptation of flowering plants to nocturnal and crepuscular pollinators. *The Quarterly Review of Biology*, **36**, 64–73.
- Basler, D. & Körner, C. (2012) Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural and Forest Meteorology*, **165**, 73–81.
- Bennie, J., Duffy, J.P., Davies, Y.W., Correa-Cano, M.E. & Gaston, K.J. (2015a) Global trends in exposure to light pollution in natural terrestrial ecosystems. *Remote Sensing*, **7**, 2715–2730.
- Bennie, J., Davies, T.W., Cruse, D., Inger, R. & Gaston, K.J. (2015b) Cascading effects of artificial light at night: resource-mediated control of herbivores in a grassland ecosystem. *Philosophical Transactions of the Royal Society of London B*, **370**, 20140131.
- Biggs, J.D., Fouche, T., Bilki, F. & Zadnikl, M.G. (2012) Measuring and mapping the night sky brightness of Perth, Western Australia. *Monthly Notices of the Royal Astronomical Society*, **421**, 1450–1464.
- Blackwell, B.F., DeVault, T.L. & Seamans, T.W. (2015) Understanding and mitigating the negative effects of road lighting on ecosystems. *Handbook of Road Ecology* (eds R. Van der Ree, D.J. Smith & C. Grilo), pp. 143–150. Wiley-Blackwell, Chichester, UK.
- Blanchard, M.G. & Runkle, E.S. (2010) Intermittent light from a rotating high-pressure sodium lamp promotes flowering of long-day plants. *HortScience*, **45**, 236–241.
- Borthwick, H.A., Hendricks, S.B., Parker, M.W., Toole, E.H. & Toole, V.K. (1952) A reversible photoreaction controlling seed germination. *Proceedings of the National Academy of Sciences of the United States of America*, **38**, 662–666.
- Briggs, W.R. (2006) Physiology of plant responses to artificial lighting. *Ecological Consequences of Artificial Night Lighting* (eds C. Rich & T. Longcore), pp. 389–412. Island Press, Washington, DC, USA.
- Cannell, M.G.R. (1997) Spring phenology of trees and frost avoidance. *Weather*, **52**, 46–52.
- Casal, J.J., Candia, A.N. & Sellaro, R. (2014) Light perception and signalling by phytochrome A. *Journal of Experimental Botany*, **65**, 2835–2845.
- Cathey, A.R. & Campbell, L.E. (1975a) Effectiveness of five vision-lighting sources on photo-regulation of 22 species of ornamental plants. *Journal of the American Society for Horticultural Science*, **100**, 65–71.
- Cathey, A.R. & Campbell, L.E. (1975b) Security lighting and its impact on the landscape. *Journal of Arboriculture*, **1**, 181–187.
- Christie, J.M. (2007) Phototropin blue-light receptors. *Annual Review of Plant Biology*, **58**, 21–45.
- CIE (1951) *Centre Internationale d'Éclairage Proceedings*, p. 37. Bureau Central de la CIE, Paris, France.
- Cinzano, P., Falchi, F. & Elvidge, C.D. (2001) The first world atlas of the artificial night sky brightness. *Monthly Notices of the Royal Astronomical Society*, **328**, 689–707.
- Coffin, A. (2007) From roadkill to road ecology: a review of the ecological effects of roads. *Journal of Transport Geography*, **15**, 396–406.
- Cousins, S.A.O. (2006) Plant species richness in midfield islets and road verges – the effect of landscape fragmentation. *Biological Conservation*, **127**, 500–509.
- Darwin, C. (1881) *The Power of Movement in Plants*. D. Appleton and Company, New York, NY, USA.
- Davies, T.W., Bennie, J. & Gaston, K.J. (2012) Street lighting changes the composition of invertebrate communities. *Biology Letters*, **8**, 764–767.
- Davies, Z.G., Fuller, R.A., Loram, A., Irvine, K.N., Sims, V. & Gaston, K.J. (2009) A national scale inventory of resource provision for biodiversity within domestic gardens. *Biological Conservation*, **142**, 761–771.
- Davies, T.W., Bennie, J., Inger, R. & Gaston, K.J. (2013) Artificial light alters natural regimes of night-time sky brightness. *Scientific Reports*, **3**, 1722.
- Eisenbeis, G. (2006) Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany. *Ecological Consequences of Artificial Night Lighting* (eds C. Rich & T. Longcore), pp. 281–304. Island Press, Washington, DC, USA.
- Eriksen, A.B., Vollsnes, A.V., Futsaether, C.M. & Kruse, O.M. (2012) Reversible phytochrome regulation influenced the severity of ozone-induced visible foliar injuries in *Trifolium subterraneum* L. *Plant Growth Regulation*, **68**, 517–523.
- Fleming, T.H., Geiselman, C. & Kress, W.J. (2009) The evolution of bat pollination: a phylogenetic perspective. *Annals of Botany*, **104**, 10176–11043.
- Fleming, T.H. & Heithaus, E.R. (1981) Frugivorous bats, seed shadows, and the structure of tropical forests. *Biotropica*, **13**, 45–53.
- Forde, D.J. & Thomas, R.G. (1966) Flowering in *Lotus pedunculatus* cav. *New Zealand Journal of Botany*, **4**, 147–152.
- Fortunato, A.E., Annunziata, R., Jaubert, M., Bouly, J.-P. & Falciatore, A. (2015) Dealing with light: the widespread and multitasking cryptochrome/photolyase family in photosynthetic organisms. *Journal of Plant Physiology*, **172**, 42–54.
- Franklin, K.A. & Whitelam, G.C. (2005) Phytochromes and shade-avoidance responses in plants. *Annals of Botany*, **96**, 169–175.
- Futsaether, C.M., Vollsnes, A.V., Kruse, O.M.O., Otterholt, E., Kvaal, K. & Eriksen, A.B. (2009) Effects of the nordic photoperiod on ozone sensitivity and repair in different clover species studied using infrared imaging. *Ambio*, **38**, 437–443.
- Gaston, K.J., Ávila-Jiménez, M.L. & Edmondson, J.L. (2013) Managing urban ecosystems for goods and services. *Journal of Applied Ecology*, **50**, 830–840.
- Gaston, K.J. & Bennie, J. (2014) Demographic effects of artificial nighttime lighting on animal populations. *Environmental Reviews*, **22**, 323–330.
- Gaston, K.J., Duffy, J.P. & Bennie, J. (2015) Quantifying the erosion of natural darkness in the global protected area system. *Conservation Biology*, **29**, 1132–1141.
- Gaston, K.J., Davies, T.W., Bennie, J. & Hopkins, J. (2012) Review: reducing the ecological consequences of night-time light pollution: options and developments. *Journal of Applied Ecology*, **49**, 1256–1266.
- van Geffen, K.G., van Grunsven, R.H.A., van Ruijven, J., Berendse, F. & Veenendaal, E.M. (2014) Artificial light at night causes diapause inhibition and sex-specific life history changes in a moth. *Ecology and Evolution*, **4**, 2082–2089.
- van Geffen, K.G., van Eck, E., de Boer, R.A., van Grunsven, R.H.A., Salis, L., Berendse, F. & Veenendaal, E.M. (2015) Artificial light at night inhibits mating in a Geometrid moth. *Insect Conservation and Diversity*, **8**, 282–287.
- Goddard, M.A., Dougill, A.J. & Benton, T.G. (2010) Scaling up from gardens: biodiversity conservation in urban environments. *Trends in Ecology and Evolution*, **25**, 90–98.
- Goto, N., Kumagai, T. & Koornneef, M. (1991) Flowering responses to light-breaks in photomorphogenic mutants of *Arabidopsis thaliana*, a long-day plant. *Physiologia Plantarum*, **2**, 209–215.
- Hanley, M.E. & Wilkins, J.P. (2015) On the verge? Preferential use of road-facing hedgerow margins by bumblebees in agro-ecosystems. *Journal of Insect Conservation*, **19**, 67–74.
- Hänninen, H. (1991) Does climatic warming increase the risk of frost damage in northern trees? *Plant, Cell and Environment*, **14**, 449–454.
- Hovd, H. & Skogen, A. (2005) Plant species in arable field margins and road verges of central Norway. *Agriculture, Ecosystems and Environment*, **110**, 257–265.
- Hunt, R. (1844) *Researches on Light: An Examination of all the Phenomena Connected With the Chemical and Molecular Changes Produced by the Influence of the Solar Rays*. Longman, Brown Green and Longmans, London, UK.
- Hunt, R. (1854) *Researches on Light in its Chemical Relations: Embracing a Consideration of all the Photographic Processes*. Longman, Brown Green and Longmans, London, UK.
- Ishikawa, R., Shinomura, T., Takano, M. & Shimamoto, K. (2009) Phytochrome dependent quantitative control of Hd3a transcription is the basis of the night break effect in rice flowering. *Genes and Genetic Systems*, **84**, 179–184.
- Johnson, K. (1979) Control of Lampenflora at Waitomo Caves, New Zealand. *Cave Management in Australia III: Proceedings of the 3rd Australasian Cave Tourism and Management Conference, Mount Gambier* (ed. A.A. Robinson), pp. 105–122. South Australian National Parks and Australian Speleological Federation, Adelaide, Australia.
- Kami, C., Lorrain, S., Hornitschek, P. & Fankhauser, C. (2010) Light-regulated plant growth and development. *Current Topics in Developmental Biology*, **91**, 29–66.

- Körner, C. & Basler, D. (2010) Phenology under global warming. *Science*, **327**, 1461–1462.
- Kyba, C.M., Tong, K.P., Bennie, J., Birriel, I., Birriel, J.J., Cool, A. *et al.* (2015) Worldwide variations in artificial skyglow. *Scientific Reports*, **5**, 8409.
- van Langevelde, F., Ettema, J.A., Donners, M., WallisDeVries, M.F. & Groenendijk, D. (2011) Effect of spectral composition of artificial light on the attraction of moths. *Biological Conservation*, **144**, 2274–2281.
- Le Viol, I., Julliard, R., Kerbiriou, C., de Redon, L., Carnino, N., Machon, N. & Porcher, E. (2008) Plant and spider communities benefit differently from the presence of planted hedgerows in highway verges. *Biological Conservation*, **141**, 1581–1590.
- Lefèvre, M. (1974) La maladie verte de Lascaux. *Studies in Conservation*, **19**, 126–156.
- Lewanzik, D. & Voigt, C.C. (2014) Artificial light puts ecosystem services of frugivorous bats at risk. *Journal of Applied Ecology*, **51**, 388–394.
- Longcore, T. & Rich, C. (2004) Ecological light pollution. *Frontiers in Ecology and the Environment*, **2**, 191–198.
- Macgregor, C.J., Pocock, M.J.O., Fox, R. & Evans, D.M. (2014) Pollination by nocturnal lepidoptera, and the effects of light pollution: a review. *Ecological Entomology*, **40**, 187–198.
- Marçais, B., Kavkova, M. & Desprez-Loustau, M.-L. (2009) Phenotypic variation in the phenology of ascospore production between European populations of oak powdery mildew. *Annals of Forest Science*, **66**, 814.
- Matzke, E.B. (1936) The effect of street lights in delaying leaf-fall in certain trees. *American Journal of Botany*, **23**, 446–452.
- Munir, S., Chen, H. & Ropkins, K. (2012) Modelling the impact of road traffic on ground level ozone concentration using a quantile regression approach. *Atmospheric Environment*, **60**, 283–291.
- Plantlife (2013) *Flowers on the edge*, available at <http://www.plantlife.org.uk/>, accessed 13th July 2015.
- Poulin, C., Bruyant, F., Laprise, M.-H., Cockshutt, A.M., Vandenhecke, J.M.-R. & Huot, Y. (2014) The impact of light pollution on diel changes in the photophysiology of *Microcystis aeruginosa*. *Journal of Plankton Research*, **36**, 286–291.
- Raven, J.A. & Cockell, C.S. (2006) Influence on photosynthesis of starlight, moonlight, planetlight, and light pollution (reflections on photosynthetically active radiation in the universe). *Astrobiology*, **6**, 668–675.
- Rivera, G. & Borchert, R. (2001) Induction of flowering in tropical trees by a 30-min reduction in photoperiod: evidence from field observations and herbarium collections. *Tree Physiology*, **21**, 201–212.
- Rockwell, N.C., Duanmu, D., Martin, S.S., Bachy, C., Price, D.C., Bhat-tacharya, D., Worden, A.Z. & Lagarias, J.C. (2014) Eukaryotic algal phytochromes span the visible spectrum. *Proceedings of the National Academy of Sciences of the United States of America*, **112**, E1051.
- Runkle, E.S., Heins, R.D., Cameron, A.C. & Carlson, W.H. (1998) Flowering of herbaceous perennials under various night interruption and cyclic light treatments. *HortScience*, **33**, 672–677.
- Sager, J.C. & McFarlane, J.C. (1997) Radiation. *Plant Growth Chamber Handbook* (eds R.W. Langhans & T.W. Tibbitts), pp. 1–29. T.W. Iowa State University Press, Iowa City, IA, USA.
- Schroeder, C.A. (1945) Tree foliation affected by street lights. *Arborists News*, **10**, 1–3.
- Sharpe, L.T., Stockman, A., Jagla, W. & Jagle, H. (2005) A luminous efficiency function, $V^*(\lambda)$, for daylight adaptation. *Journal of Vision*, **5**, 948–968.
- Sinnadurai, S. (1981) High pressure sodium lights affect crops in Ghana. *World Crops*, **33**, 120–122.
- Smith, H. (1982) Light quality, photoperception and plant strategy. *Annual Review of Plant Physiology*, **33**, 481–518.
- Song, Y.H., Ito, S. & Imazuimi, T. (2010) Similarities in the circadian clock and photoperiodism in plants. *Current Opinion in Plant Biology*, **13**, 594–603.
- Spellerberg, I. (1998) Ecological effects of roads and traffic: a literature review. *Global Ecology and Biogeography*, **7**, 317–333.
- Stone, E.L., Jones, G. & Harris, S. (2009) Street lighting disturbs commuting bats. *Current Biology*, **19**, 1–5.
- Stone, E.L., Jones, G. & Harris, S. (2012) Conserving energy at a cost to biodiversity? Impacts of LED lighting on bats. *Global Change Biology*, **18**, 2458–2465.
- Tikka, P.M., Högmänder, H. & Koski, P.S. (2001) Road and railway verges serve as dispersal corridors for grassland plants. *Landscape Ecology*, **16**, 659–666.
- Trombulak, S.C. & Frissell, C.A. (2000) Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology*, **14**, 18–30.
- Tyser, R.W. & Worley, C.A. (1992) Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (U.S.A.). *Conservation Biology*, **6**, 253–262.
- Van Asch, M., Van Tienderen, P.H., Holleman, L.J.M. & Visser, M.E. (2007) Predicting adaptation of phenology in response to climate change, an insect herbivore example. *Global Change Biology*, **13**, 1596–1604.
- Visser, M.E. & Holleman, L.J. (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London B*, **268**, 289–294.
- Vollsnes, A.V., Eriksen, A.B., Otterholt, E., Kvaal, K., Oxaal, U. & Futsaether, C.M. (2009) Visible foliar injury and infrared imaging show that daylength affects short-term recovery after ozone stress in *Trifolium subterraneum*. *Journal of Experimental Botany*, **60**, 3677–3686.
- Warrant, E. & Dacke, M. (2011) Vision and visual navigation in nocturnal insects. *Annual Review of Entomology*, **56**, 239–254.
- Wesołowski, T. & Rowiński, P. (2006) Tree defoliation by winter moth *Operophtera brumata* L. during an outbreak affected by structure of forest landscape. *Forest Ecology and Management*, **221**, 1–3.
- Whitman, C.M., Heins, R.D., Cameron, A.C. & Carlson, W.H. (1998) Lamp type and irradiance level for daylength extensions influence flowering of *Campanula carpatica* ‘Blue Clips’, *Coreopsis grandiflora* ‘Early Sunrise’, and *Coreopsis verticillata* ‘Moonbeam’. *Journal of the American Society of Horticultural Science*, **123**, 802–807.

Received 14 July 2015; accepted 27 January 2016

Handling Editor: Nathan Swenson