

## Hypothesis Paper

# Influence on Photosynthesis of Starlight, Moonlight, Planetlight, and Light Pollution (Reflections on Photosynthetically Active Radiation in the Universe)

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### ABSTRACT

Photosynthesis on Earth can occur in a diversity of organisms in the photosynthetically active radiation (PAR) range of 10 nmol of photons  $\text{m}^{-2} \text{s}^{-1}$  to 8 mmol of photons  $\text{m}^{-2} \text{s}^{-1}$ . Similar considerations would probably apply to photosynthetic organisms on Earth-like planets (ELPs) in the continuously habitable zone of other stars. On Earth, starlight PAR is inadequate for photosynthetically supported growth. An increase in starlight even to reach the minimum theoretical levels to allow for photosynthesis would require a universe that was approximately ten million times older, or with a ten million times greater density of stars, than is the case for the present universe. Photosynthesis on an ELP using PAR reflected from a natural satellite with the same size as our Moon, but at the Roche limit, could support a low rate of photosynthesis at full Moon. Photosynthesis on an ELP-like satellite of a Jupiter-sized planet using light reflected from the planet could be almost 1% of the rate in full sunlight on Earth when the planet was full. These potential contributions to photosynthesis require that the contribution is compared with the rate of photosynthesis driven by direct radiation from the star. Light pollution on Earth only energizes photosynthesis by organisms that are very close to the light source. However, effects of light pollution on photosynthesis can be more widespread if the photosynthetic canopy is retained for more of the year, caused by effects on photoperiodism, with implications for the influence of civilizations on photosynthesis. **Key Words:** Photosynthetically active radiation—Photosynthesis—Lunar—Olbers Paradox—Earth-like planets. *Astrobiology* 6, 668–675.

### INTRODUCTION

**P**HOTOSYNTHESIS IS THE MAIN energetic driver of biology on Earth. In the absence of the biological catalysis of the light-energized conversion of carbon dioxide, water, and other inorganic resources into organic matter and oxygen, the Earth

would support a much less complex biosphere, with several orders of magnitude smaller energy and information fluxes (Jakosky and Shock, 1998; Wolstencroft and Raven, 2002). It is highly likely that a similar situation would prevail on other Earth-like planets (ELPs): non-photosynthetic energy sources, such as exergonic inorganic chem-

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ical reactions driving growth of chemolithotrophs, or abiologically produced organic matter used by chemoorganotrophs, could only support less complex biospheres (Jakosky and Shock, 1998; Wolstencroft and Raven, 2002).

Wolstencroft and Raven (2002) showed that photosynthetic rates on ELPs in the continuously habitable zone (CHZ) of a number of spectral classes of stars could be within an order of magnitude or so of those on Earth, at least on the basis of photosynthetically active radiation (PAR) (400–700 nm) requirements of photosynthesis on Earth. Relaxing these wavelength requirements to take into account spectral variations among stars did not significantly alter this conclusion (Wolstencroft and Raven, 2002; Raven and Wolstencroft, 2004).

These types of modeling exercises (Wolstencroft and Raven, 2002; Cockell and Raven, 2004; Raven and Wolstencroft, 2004) deal only with electromagnetic radiation from the star that the ELP is orbiting. The present paper expands the analysis to include the possibility of using PAR from distant stars, PAR reflected from natural satellites, or PAR from human sources on Earth.

We begin by outlining the ranges of photon flux densities of PAR at which photosynthesis can occur on Earth, and then consider starlight followed by moonlight and human-produced light. We do not consider deep-ocean PAR, which can arise from the short wavelength tail of the thermal emission from hydrothermal vents, chemoluminescence from the abiotic oxidation of sulfide by oxygen, and from sonoluminescence, which could potentially drive photosynthesis (Raven *et al.*, 2000; Wolstencroft and Raven, 2002; Beatty *et al.*, 2005).

#### THE RANGE OF FLUXES OF PAR AT WHICH PHOTOSYNTHESIS CAN OCCUR ON EARTH AND (PROBABLY) ELSEWHERE

A number of observations and theoretical considerations have been brought to bear on the question of the minimum PAR needed for photolithotrophic growth (Radmer and Kok, 1977; Raven and Beardall, 1982; Tett, 1990; Raven *et al.*, 2000; Hauss *et al.*, 2002; Wolstencroft and Raven, 2002; Quigg and Beardall, 2003; Quigg *et al.*, 2003; Cockell and Raven, 2004; Raven and Wolstencroft, 2004). For growth with O<sub>2</sub>-evolving photosynthesis as the solar energy transducer, the likely mini-

mum is 0.1  $\mu\text{mol}$  of photons  $\text{m}^{-2} \text{s}^{-1}$ , with an absolute minimum of 0.01  $\mu\text{mol}$  of photons  $\text{m}^{-2} \text{s}^{-1}$  (Raven *et al.*, 2000; Wolstencroft and Raven, 2002; Cockell and Raven, 2004). The values may be significantly lower for the growth of organisms using electron donors other than water, *e.g.*, sulfide in the case of green sulfur bacteria (Raven *et al.*, 2000; Beatty *et al.*, 2005; Manske *et al.*, 2005). As for the upper limit, this is clearly severalfold higher than the maximum natural PAR on Earth (2 mmol of photons  $\text{m}^{-2} \text{s}^{-1}$ ), *i.e.*, up to 8 mmol of photons  $\text{m}^{-2} \text{s}^{-1}$  for at least some photosynthetic organisms (Wolstencroft and Raven, 2002).

The experimentation and, to some extent, the modeling on which these conclusions on minimum and maximum values of PAR for photosynthetic growth are based come from photosynthetic organisms on Earth. However, by considering the fundamental biophysics of the photosynthetic process, Wolstencroft and Raven (2002) concluded that similar constraints would apply to the evolution of photosynthesis on ELPs.

#### PHOTOSYNTHESIS USING PAR FROM DISTANT STARS?

The origin of the universe in the Big Bang some 15 billion years ago involved the generation of free subatomic particles that were able to form atomic nuclei of H, He, and (probably) Li, and then atoms of these elements as the expanding volume of matter cooled (Bromm and Larson, 2004). Further cooling led to the cosmic dark ages when there was no source of electromagnetic radiation in the universe other than the background radiation from the Big Bang. These dark ages lasted several hundred million years and were ended when the first stars formed, which generated heavier elements (“metals” in the terminology of astronomers) and heat, and thence electromagnetic radiation by nuclear reactions (Bromm and Larson, 2004; Iwamoto *et al.*, 2005). It was only after this first generation of stars had become supernovas, dispersing the “metals” and allowing planets to form, would ELPs have been formed.

The only example that we have of an ELP with photosynthesis is the Earth, where photosynthesis is energized by light from the Sun. Starlight flux in the PAR wavelength range, *i.e.*, radiation 400–700 nm at the Earth’s surface on a moonless night in an area not affected by human light pollution, is about 1 fmol of photons  $\text{m}^{-2} \text{s}^{-1}$  when the sky is clear, and about 0.1 fmol of photons  $\text{m}^{-2} \text{s}^{-1}$  when

the sky is overcast (Munz and McFarland, 1973). This means that even the most favorably presented photosynthetic organism at the land or sea surface would not be able to photosynthesize in starlight. The very low flux of starlight has been a subject of interest for several centuries, but is generally known as "Olbers's Paradox" after the 1826 publication by the German scientist Olbers (Wesson, 1991). A universe that is infinite in extent and age, and with a uniform density of stars, should have a spatially invariant radiant flux: the inverse square law for the decrease in photon flux with distance of radiation sources (stars) from an observer would be exactly offset by the increasing number of stars in successive shells further from the observer. It is clear (Wesson, 1991) that the explanation of Olbers's Paradox is mainly due to the finite age of the universe in conjunction with the finite speed of light, with the expansion of the universe as a second-order effect; there has not yet been time for the universe to be flooded with radiant energy in the way Olbers hypothesized.

The analysis by Wesson (1991) shows that in an infinite universe with the same density of galaxies as in the observable universe (a sphere with a radius in light-years equal to the age of the universe), an increase in starlight by seven orders of magnitude would require that the universe is seven orders of magnitude older than its actual age of about 15 billion years, if PAR on Earth from starlight was to reach the absolute minimum for photosynthesis—about  $0.01 \mu\text{mol of photons m}^{-2} \text{s}^{-1}$ . Alternatively, for a universe that is 15 billion years old, the observable universe would need to have a ten million fold increase in the density of galaxies with the presently observed density of stars in each galaxy, or in the density of stars with the presently observed density of galaxies, to yield PAR of up to  $0.01 \mu\text{mol of photons m}^{-2} \text{s}^{-1}$  (Wesson, 1991). This shows that very large changes to the universe would be required to yield a starlight PAR that could make even a minimal impact on primary producers adapted to an Earth surface PAR of up to  $2 \text{ mmol of photons m}^{-2} \text{s}^{-1}$ .

### PHOTOSYNTHESIS USING PAR REFLECTED FROM (A) NATURAL SATELLITE(S)?

#### *The Earth's Moon: background*

The Moon is the sixth most massive satellite of the 63 (at least) in the solar system (Peale, 1999).

It is by far the most massive relative to the planet it is orbiting, with 12% of the mass of the Earth (Peale, 1999).

The Moon clearly has important effects on life on Earth, *e.g.*, via tidal, semilunar, and lunar rhythmicity in marine organisms (Smith, 1982; Lüning, 1990; Yamihara, 2004). The influences have changed over time as the Moon has receded from the Earth and the Earth's daylength has increased, with a corresponding decrease in the frequency and amplitude of oceanic lunar tides (Proudman, 1952; Peale, 1999). While the amplitude of oceanic lunar tides on Earth is, other things being equal, linearly related to the inverse of the cube of the Earth–Moon distance, a number of considerations mean that the tidal amplitude just after the Moon's formation was less than this prediction. The greater rate of rotation of the Earth just after the Moon was formed may also have altered mean wind speed and, hence, the depth of the upper mixed layer in the ocean, with implications for phytoplankton photosynthesis (Tett, 1990).

More controversially, the Moon-forming impact event (Peale, 1999; Canup, 2004) could be construed as an important factor in the extent of plate tectonic activity and, hence, of climate stability (Kasting and Catling, 2003) due to removal of crustal material from the Earth to form the Moon. It has also been suggested (Laskar *et al.*, 1993; but see Cockell, 2003) that stabilization of the Earth's obliquity by the Moon is essential for climate stability and, hence, for the occurrence of land-based life (Laskar *et al.*, 1993; Kasting and Catling, 2003).

It is clear that solar radiation reflected by the Moon can be sensed by organisms on Earth, and the informational role of moonlight is not in doubt (Munz and McFarland, 1973; Salisbury, 1981; Smith, 1982; Gorbunov and Falkowski, 2002). The aspect of the biological effects of the Moon we consider here is the possibility that moonlight could be a significant energy source for photosynthesis, both for the present day and during the ancient past when the Moon was much closer to the Earth. We also consider whether light reflected from a satellite could support photosynthesis on any tidally locked ELPs orbiting in the CHZ of main sequence stars of spectral type M.

#### *The maximum PAR of moonlight on the present Earth*

The three most reliable estimates of the PAR from full moonlight are those of Munz and Mc-

Farland (1973), Salisbury (1981) and Gorbunov and Falkowski (2002). Expressed in terms of photon flux density, these maximum values are, respectively, 0.5 nmol of photons  $\text{m}^{-2} \text{s}^{-1}$ , 3 nmol of photons  $\text{m}^{-2} \text{s}^{-1}$ , and 5 nmol of photons  $\text{m}^{-2} \text{s}^{-1}$ . These values are less than the absolute minimum for photolithotrophic growth by  $\text{O}_2$ -evolving organisms (10 nmol of photons  $\text{m}^{-2} \text{s}^{-1}$ ), so that even the full Moon on a cloudless night could not support photosynthetic growth of organisms at the ocean or land surface. The situation is made worse if clouds, and the lunar cycle, are taken into account.

An alternative approach to estimating the PAR from moonlight is to use the solar energy incident on the Moon, the Moon's albedo, and the fraction of the reflected radiation that is intercepted by the Earth. The Sun emits  $3.9 \times 10^{26} \text{ J s}^{-1}$  of total electromagnetic radiation. The surface area of a sphere with a radius equal to that of the orbit of the Earth–Moon system ( $1.49 \times 10^{11} \text{ m}$ ) is  $2.79 \times 10^{23} \text{ m}^2$ , so that the radiation flux incident on a square meter of the Moon, or the top of the Earth's atmosphere, perpendicular to solar radiation is  $3.9 \times 10^{26} / 2.7 \times 10^{23}$  or  $1.4 \times 10^3 \text{ J m}^{-2} \text{s}^{-1}$  (= the solar constant). The radius of the Moon is  $1.74 \times 10^6 \text{ m}$ , so the projected area is  $9.48 \times 10^{12} \text{ m}^2$  and the total solar radiation intercepted is  $9.48 \times 10^{12} \times 1.4 \times 10^3$  or  $1.33 \times 10^{16} \text{ J s}^{-1}$ . The lunar albedo, with little dependence on wavelength, is 0.1, so the reflected radiation is  $1.33 \times 10^{15} \text{ J s}^{-1}$ . This reflected radiation is dispersed radially over the area above the illuminated face of the Moon. The surface area of a hemisphere with a radius equal to the Moon–Earth distance ( $3.48 \times 10^8 \text{ m}$ ) is  $7.60 \times 10^{17} \text{ m}^2$ , so the radiation reflected from the Moon incident of a square meter of the Earth's projected area is  $1.33 \times 10^{15} / 7.60 \times 10^{17}$  or  $1.75 \times 10^{-3} \text{ J m}^{-2} \text{s}^{-1}$ . The solar constant of  $1.4 \times 10^3 \text{ J m}^{-2} \text{s}^{-1}$  is equivalent to a maximum PAR at the land or sea surface of  $2 \times 10^{-3} \text{ mol of photons m}^{-2} \text{s}^{-1}$  PAR, so the computed radiation flux of moonlight is equal to  $(1.75 \times 10^{-3} \times 2 \times 10^{-3}) / 1.4 \times 10^3$  or 2.5 nmol of photons  $\text{m}^{-2} \text{s}^{-1}$ . For PAR at the top of the Earth's atmosphere this value applies to the full Moon; the PAR at the new Moon is, of course, zero. This full Moon value calculated from astronomical data agrees well with the range of PAR values of moonlight at full moon of 0.5–5 nmol of photons  $\text{m}^{-2} \text{s}^{-1}$ , based on measurements at the Earth's surface.

While moonlight is not a significant source of energy for photosynthesis on Earth today, there

is the question as to what happened earlier in the evolution of life when the Moon was much closer to the Earth?

Even if present-day moonlight cannot provide sufficient energy for photosynthesis, it could still increase photosynthesis by informational effects on photosynthetic organisms if moonlight altered the production, retention, or functional competence of the photosynthetic apparatus. Gorbunov and Falkowski (2002) showed that the blue component of moonlight could cause contraction of polyps in corals that normally have their tentacles extended at night. However, this behavior occurs in corals with few or no photosynthetic dinoflagellate symbionts; contraction at night, and tentacle extension in daylight is typical of corals with a greater density of symbionts and a greater capacity for photosynthesis (Gorbunov and Falkowski, 2002). Bünning and Moser (1969) suggested that the nyctinastic leaf folding of legumes was a means of preventing moonlight from activating the red form of the pigment phytochrome in the upper leaf epidermis by interposing the leaf mesophyll, with a high absorptance in the red region of the spectrum, between phytochrome and moonlight. However, there is as yet no experimental evidence for this suggestion. The possibility that light absorbed by pigments other than photosynthetic pigments could increase the amount of photosynthesis possible in sunlight is also considered below under light pollution.

#### *The maximum PAR of moonlight on Earth if the Moon was at the Roche Limit*

The Roche Limit is the closest orbit around a planet if a “fluid” satellite is to be formed by accretion, or, once formed, is to avoid being broken up by the planet's gravitational field. A number of formulations of the equation that describes this limit are available, all giving similar limits for a given set of characteristics of the planet and the satellite. We use the equation in Peale (1999), which, for the masses of the Earth and the Moon, gives a Roche Limit of 2.9 times the radius of the Earth or 18,500 km (center of the Earth to center of the Moon).

While we do not suggest that the Moon was ever as close to the Earth as the Roche Limit, it is worth considering the level of PAR from moonlight that would reach the Earth's surface if the Moon was at the Roche limit—to give an upper



limit of the potential for moonlight to support photosynthesis early in the history of life on Earth. Such estimates must take into account the Faint Young Sun: the Sun was 30% less bright than it is today when it formed some 4.6 Ga ago (Kasting and Catling, 2003), and ~25% less bright 3.7 Ga ago when life may have become established on Earth (*e.g.*, Cockell, 2003). We assume that the lunar albedo for PAR has been constant over this time period; Dobber *et al.* (1998) obtained values of 0.05 at 240 nm to 0.28 at 800 nm for observations in 1995.

The Earth–Moon distance is currently 384,400 km. Applying the inverse square law means that the PAR of full moonlight at the Earth's surface with the Moon at the Roche Limit 3.7 Ga ago is  $0.75 \times (384,400/18,500)^2$  or 323 times the present value. This would give full moonlight PAR values in the range 162–1620 nmol of photons  $\text{m}^{-2} \text{s}^{-1}$ . At least the high end of this range of values could permit photosynthesis at the ocean or land surface under a full Moon on a cloudless night. However, it would not seem likely that this possibility would have had a significant effect on the evolution of photosynthesis on Earth, since the maximum PAR from sunlight 3.7 Ga ago was 1,500  $\mu\text{mol}$  of photons  $\text{m}^{-2} \text{s}^{-1}$ , and sunlight was not and is not subject to variation with the lunar cycle (eclipses excepted). Sunlight would have allowed photosynthesis down to at least 100 m in clear water, and on land. Photosynthesis even in sunlight would have been compromised in the oceanic benthos with the Moon at the Roche Limit because of the tidal amplitude, and in the pelagic by the large mixing depth related to high wind speeds. These effects would have been smaller for an ELP with a satellite similar to our Moon, but with a lower angular momentum for the ELP–satellite system resulting from a different configuration of the satellite-forming impact from the one that formed the Earth's Moon (see Kasting and Catling, 2003).

An ELP with a Moon-like satellite, but with the lower angular momentum mentioned above and with the additional constraint of orbiting a M spectral class star [where the CHZ involves an ELP having its rotation tidally locked so as to always present the same face to the star (*e.g.*, Kasting and Catling, 2003)], is the final case to be considered for moonlight-powered photosynthetic growth.

### *Moonlight and photosynthesis on a tidally locked ELP orbiting an M dwarf star*

Tidally locked ELPs orbiting M stars have one face continually facing the star, so any photosynthesis on the other side of the planet would have to be driven by PAR reflected from a satellite. In such a case it would be possible for direct selection for photosynthesis in moonlight to occur since populations of organisms on the side of the planet not facing the star could be genetically isolated from those on the sunny side. The modeling of Joshi *et al.* (1997) shows that the “dark” hemisphere of the planet could be kept warm enough to prevent the ocean and atmosphere from freezing if the atmosphere were dense enough to allow sufficient heat transfer from the sunny side. The low surface temperature of M stars gives a spectral output biased toward longer wavelengths, which has implications with regard to (a) the number of photons needed to move one electron from water to carbon dioxide, (b) reaction centers operating with relatively low-energy photons, and (c) the effect of atmospheric and oceanic water in absorbing the longer wavelengths of PAR applicable to those organisms (Wolstencroft and Raven, 2002; Raven and Wolstencroft, 2004). These considerations mean a lower potential for photosynthesis for an ELP orbiting a M star than for an F or G main-sequence star.

Another aspect of M dwarf stars is the occurrence of ultraviolet (UV) radiation flares early in their (long) life, superimposed on the low steady-state UV radiation output. This would have implications for the evolution of photosynthesis using direct radiation from the star in terms of the need for UV radiation screening (Raven and Wolstencroft, 2004). For photosynthesis powered by moonlight, the albedo of a moon resembling Earth's would be lower in the UV radiation than at longer wavelengths (Dobber *et al.*, 1998), so moonlight may avoid some of the problems associated with flares of UV radiation.

This analysis of the potential for moonlight-driven photosynthesis on an ELP in the CHZ of an M dwarf star assumes that such ELPs can have satellites. The possibility of the occurrence, and the orbit, of any such moons needs scrutiny. For moonlight-powered photosynthesis, any moon would need to be near to the Roche limit and have been formed by an impact that did not impart as much angular momentum to the ELP–satellite

system as is present in the Earth–Moon system because of the consideration of large oceanic tidal amplitude on benthic and, via winds and mixing depth, planktonic photosynthetic productivity. In any case, the photosynthetic primary productivity on the hemisphere not exposed to the M dwarf could not exceed 1% of that powered by solar radiation on Earth even under the most favorable assumptions (Wolstencroft and Raven, 2002).

### PHOTOSYNTHESIS ON A MOON USING PAR REFLECTED FROM THE PARENT PLANET

The Earth's Moon cannot support photosynthetic organisms for reasons other than that of the supply of PAR, *e.g.*, lack of liquid water and an atmosphere, unless appropriately controlled environments are constructed by people. The larger projected area (13.5 times) and the higher albedo (2.5 times) of the Earth than of the Moon mean that the maximum Earthlight PAR on the Moon is 33 times higher than the maximum moonlight PAR on Earth, *i.e.*, 82.5 nmol of photons  $\text{m}^{-2} \text{s}^{-1}$ . This is rather higher than the minimum PAR required for photosynthesis on Earth, and the episodes of earthlight in the lunar night may be able to permit a very low rate of photosynthesis in a controlled environment, supplementing photosynthesis using sunlight in the lunar day.

More relevant to photosynthesis on a moon in the absence of intervention by intelligent beings is the hypothesized case of a moon equivalent to an ELP orbiting a Jupiter-sized planet in the CHZ, with the planet at the same distance from the parent planet as the Earth is from the Sun. Here, the trade-off between the Roche Limit for the minimum distance for stability of a moon orbiting the planet and the projected area of the planet for intercepting and reflecting PAR from the parent star means that a higher flux of PAR reaches unit area of the ELP-like satellite. The Roche Limit for Jupiter does not exceed  $2 \times 10^8 \text{ m}$ , and the radius of the orbit of Io is  $4.2 \times 10^8 \text{ m}$ . For an ELP moon at  $4.2 \times 10^8 \text{ m}$  from the planet the surface area of the hemisphere with this radius is  $1.1 \times 10^{18} \text{ m}^2$ . The projected area of Jupiter is 1,578 times that of the Earth's Moon, so the  $2.1 \times 10^{19} \text{ J s}^{-1}$  reflected from the planet assuming an albedo of 0.1 is equivalent to  $2.1 \times 10^{18} / 1.1 \times 10^{18}$  or  $1.9 \text{ J m}^{-2} \text{s}^{-1}$  at right angles to the reflected radiation at the top of the atmosphere of the ELP-like moon when

the planet is full. Conversion to PAR, assuming the solar constant of  $1.3 \times 10^3 \text{ J m}^{-2} \text{s}^{-1}$ , equals  $2 \text{ mmol m}^{-2} \text{s}^{-1}$  PAR; thus, the PAR on a surface at the ELP-like moon's surface at right angles to the reflected radiation is  $2.9 \mu\text{mol}$  of photons  $\text{m}^{-2} \text{s}^{-1}$ . For an ELP-like moon closer to the Roche Limit, with an orbit of radius  $2 \times 10^8 \text{ m}$ , the PAR at right angles to the reflected radiation in full planetlight is  $8.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ .

This is significantly higher than the minimum PAR required for photosynthesis on Earth; episodes of planetlight in the Moon's night could permit a low rate of photosynthesis, supplementing photosynthesis using sunlight in the Moon's day.

These considerations show that photosynthesis on a natural satellite could occur using PAR reflected from the parent planet during the satellite's night, supplementing the photosynthesis using direct sunlight during the satellite's day. However, it must be remembered that most photosynthetic organisms on Earth have a relatively limited PAR range (usually less than two orders of magnitude) over which they show effective acclimation of their photosynthetic apparatus, though photosynthetic organisms as a whole can exploit at least four orders of magnitude of flux densities of PAR (Raven and Geider, 2003).

### PHOTOSYNTHESIS USING PAR FROM ARTIFICIAL SOURCES

Light produced by humans that could influence photosynthesis can be divided into light pollution, *i.e.*, PAR (or other wavelengths or irradiances of radiation) produced for reasons other than increasing photosynthesis (Cinzano *et al.*, 2001, 2002; Navisada and Schreuder, 2004), and PAR (or other wavelengths or irradiances of electromagnetic radiation) specifically generated to increase photosynthesis.

Light pollution only provides a flux of PAR that will significantly increase the rate of photosynthesis if the light source is very intense or very close to the photosynthetic organism. These criteria are rarely met, and the effect of light pollution on photosynthesis is generally indirect via effects on plant phenology. Leaf abscission in annually deciduous vascular plants is frequently under photoperiodic control, with abscission occurring in short days. Daylength extension by street lamps or security lamps can delay leaf ab-

scission (illustrated as the frontispiece of Salisbury, 1963) and thus extend the length of the growing (photosynthesizing) season. However, such an increase in leaf area duration could cause problems for plants if there is a leaf-damaging frost while leaves are still photosynthetically active and before nutrients have been withdrawn to the perennial parts of the plant, thereby restricting leaf area development in the next growing season.

In a recent study, Cinzano *et al.* (2001) investigated sky brightness caused by light pollution using the Defense Meteorological Satellite Program. By mapping sky brightness they determined that half of the world population now live under a night sky that is brighter than astronomers measure under the first quarter Moon. Remarkably, one-quarter of the world population live in areas where the night sky is brighter than the full Moon. These light levels alone are still too low to drive photosynthesis. However, added to the maximum flux of PAR estimated from the full Moon (giving a total in excess of  $10 \text{ nmol of photons m}^{-2} \text{ s}^{-1}$ ), they bring the total flux close to the lower limits for photosynthesis. This raises the intriguing theoretical possibility of anthropogenic light around particularly well-illuminated metropolises in combination with full Moon light being theoretically sufficient to drive photosynthesis.

Glasshouses and related structures frequently have electromagnetic radiation sources to increase photosynthesis (*e.g.*, daylength extension and daylight supplementation in high latitudes in winter), as well as manipulation of the photoperiod to produce marketable material from photoperiodically controlled crop plants at the required time of year. This has been extended (as night-break illumination) to crops such as chrysanthemums grown outdoors, although with illumination arrangements much as for the same crop in glasshouses (see Paleg and Aspinall, 1970). Experimental use has been made of flood-lamps and of lasers as night-break illumination in lower-value extensively grown crops such as barley (Paleg and Aspinall, 1970). Lasers could be more energy-effective in terms of running costs since their output can be spectrally matched to the plant pigment involved, *e.g.*, the helium-neon laser used by Paleg and Aspinall (1970) to excite the red-absorbing form of the plant pigment phytochrome, which is involved in photomorphogenesis, photoperiodism, and photoregulatory phenomena (Smith, 1982).

Some regions of the Earth have been considered for *deliberate* illumination from artificial satellites. The Russian Znamya (Banner) project was directed at illuminating a small area of the night side of Earth with sunlight using an orbiting mirror. While the planned deployment on 5 February 1999 of the mirror from the Mir space station failed, theoretical considerations of this possibility are being pursued (Ashurley, 2000). These projects could potentially provide artificial sources of light for photosynthetic organisms that happen to fall under their illuminated areas.

## CONCLUSION

PAR impinging on planetary surfaces from the parent star is overwhelmingly the largest potential source of electromagnetic energy for photosynthetic biota. However, our calculations suggest that it represents just one potential source of light that may be able to drive photosynthesis. The assessment of planets and moons as "habitable" environments for photosynthetic organisms requires a more in-depth investigation of orbital parameters and planetary albedos than purely the PAR output of the parent star. Finally, the emergence of intelligent civilizations may itself influence the opportunities and constraints on photosynthetic organisms co-existing with them.

## ABBREVIATIONS

CHZ, continuously habitable zone; ELP, Earth-like planet; PAR, photosynthetically active radiation; UV, ultraviolet.

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