

# The Feasibility of Photosynthesis on Extrasolar Planets: A Primer and Review

By

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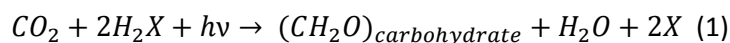
## Introduction

On Earth, photosynthetic organisms are by far the most productive primary producers on the planet. The advent of photosynthetic life has drastically changed the composition and redox chemistry of our atmosphere (Catling et al., 2001) and even the surface reflectance spectra of our planet (Tinetti et al., 2006). Because one of the most fundamental goals of astrobiology is to detect extraterrestrial life on planets like the Earth, we must pay special attention to the role of photosynthesis in potential alien biospheres. This is not easy: the study of extraterrestrial photosynthesis necessarily involves the combined contribution of the fields of molecular biology, biochemistry, atmospheric science, and stellar astrophysics. This paper will introduce the reader to the basic physical, chemical and biological underpinnings of this emerging interdisciplinary field. We will begin with an overview of the chemistry and physics of photosynthesis including the processes and limits observed for photosynthetic life on Earth. We will then discuss the feasibility of photosynthesis on worlds around other stars, providing some background information on stellar spectra, habitable zones, and the effects of planetary atmospheres. Some implications for detecting biosignatures from these worlds will be included in the discussion, but in the interest of brevity will not be the focus. We draw heavily from the work of Nancy Kiang and colleagues from two papers published in *Astrobiology*, “Spectral Signatures of Photosynthesis I: Review of Earth Organisms” (hereto referred to as Kiang et al. Paper I) and “Spectral Signatures of Photosynthesis II: Coevolution with Other Stars and the Atmosphere on Extrasolar Worlds” (hereto referred to as Kiang et al. Paper II) and references therein, although our focus will tend more towards an explanation of the scientific context than a strict presentation of their results.

## Overview of Photosynthesis

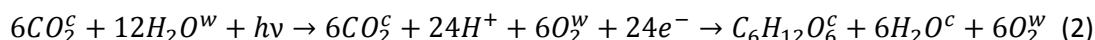
### *Photosynthetic Chemistry*

Photosynthesis converts electromagnetic radiation (light) into the electrochemical energy necessary for reducing CO<sub>2</sub> to produce organic carbon. Photosynthetic pigments in a cell are excited by photons of light, allowing the transfer of electrons through biochemical pathways (photosystems). This facilitates the redox reactions required to produce organic compounds. The general empirical chemical equation for photosynthesis is:



Where  $H_2X$  is a reducing agent (i.e.  $H_2O$ ,  $H_2S$  or  $H_2$ ) and  $h\nu$  is the energy per photon ( $h$  being Planck's constant and  $\nu$  being the frequency of the photon).

Oxygenic (oxygen-producing) photosynthesis uses water as the reductant. The stoichiometry of the above equation becomes a balanced molecular equation:



where  $C_6H_{12}O_6$  is glucose and we use the convention of Kiang et al (Paper I) by indicating the source of oxygen with a "c" or "w" superscript for carbon or water, respectively. We can see from the above equation (assuming one electron is produced for every photon absorbed) that it takes four photons to produce one  $O_2$ . An intermediate step requires four photons to reduce two molecules of coenzyme  $NADP^+$  needed to reduce one  $CO_2$  for a total of eight photons necessary to produce one  $O_2$  and fix one  $CO_2$ , at minimum (Kiang et al, Paper I). Inefficiencies present in the biochemical pipeline, in addition to photon requirements for other reactions, may increase the number of photons necessary for this reaction in practice to 12 (Govindjee, 1999; Joliot & Joliot, 2002; Munekage *et al.*, 2004). This process must be repeated six times to reduce six carbons into glucose.

Anoxygenic photosynthesis uses a different reductant than water; for example,  $H_2$ ,  $H_2S$ , or  $Fe^{2+}$ . The photon requirement for these reactions will be the same as above. Photosynthesis on Earth, and presumably on any world, requires a carbon source, a reductant, and light energy to produce carbohydrates and oxidized forms of the reductant. From an astrobiological perspective, it is useful to know the required photosynthetic inputs (to determine what worlds may have the required composition for photosynthetic life) and outputs (to facilitate detection of these processes).

#### *Photosynthetic processes in life*

Above we have described the very basic chemical inputs and outputs for photosynthesis; however, we must also explain the redox pathways in the pigments and reaction centers of the cell that facilitate the conversion of photon energy to chemical energy. A full review of these processes is outside the scope of this paper, so we refer the reader to two textbooks in the literature (Blankenship, 2002; Ke, 2001). We provide a basic explanation.

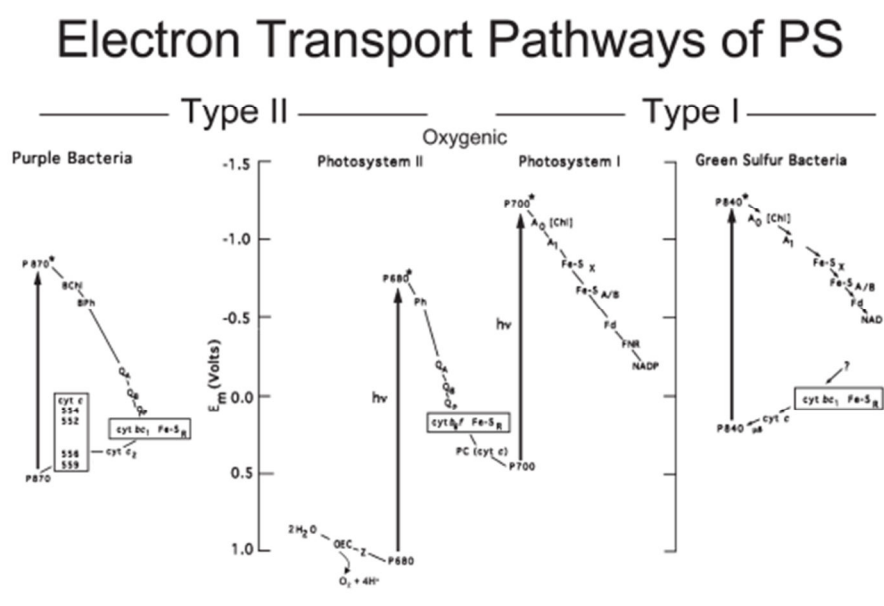
Blankenship separates photosynthesis into four phases:

(1) Light absorption and energy delivery by antenna systems, (2) primary electron transfer in reaction centers, (3) energy stabilization by secondary processes, and (4) synthesis and export of stable products.

These phases are accomplished by protein complexes called photosystems. Oxygenic photosynthesis utilizes photosystem II to oxidize water and remove electrons and photosystem I to reduce  $NADP^+$ , which is utilized via the Calvin-Benson cycle to synthesize ATP. This is known as the Z-Scheme (Blankenship and Prince, 1985). It is important to note (as will become clear later) that photosystem I

peaks in absorbance at 700 nm and photosystem II peaks at 680 nm. The antenna pigments absorb the light at shorter wavelengths (higher energy) and cascade this energy to longer wavelengths with overlapping pigments with different excitation energies until a photon is produced near the peak absorbance value of the photosystem. We reproduce a figure from Kiang et al (Paper 1) illustrating the electron transport pathways of the photosystems (Fig. 1). Note that anoxygenic photosynthesis is known to use one photosystem or the other, but not both.

Oxygenic photosynthesis on Earth uses light in the spectral region of 400-700 nm, also known as the photosynthetic active region (PAR). This seems to be an evolutionary adaptation to take advantage of the abundant light that reaches the Earth's surface at these wavelengths due to both its high initial production in the solar photosphere and Earth's atmospheric window in this spectra region (see following discussion).



**Fig 1.** – Electron transport pathways of photosynthesis. The axes indicate the midpoint redox potentials for excited and ground states of the reaction centers for intermediate and reduced products. Schemes for oxygenic photosynthesizers as well as purple and green sulfur bacteria are shown. Figure from Kiang et al (Paper 1).

### Limits of photosynthesis

If we desire to understand the feasibility, distribution, and characteristics of photosynthetic life living under the light of other stars, we must first understand and attempt quantify the limits of photosynthesis. Photosynthetic life, like all life, will be limited by physical conditions (e.g. temperature, pressure) and biogeochemical factors (e.g. redox state, nutrient availability). Life on Earth has shown to be adapted to a wide range of extreme environmental conditions (Rothschild & Mancinelli, 2001). Photosynthetic life in particular has shown temperature tolerance from  $-15.7^\circ\text{C}$  (the lower survival limit for arctic snow algae and cyanobacteria; Gorton et al, 2001) to  $75^\circ\text{C}$  for photosynthetic bacteria in hot springs (Miller et al, 1998). This is the temperature at which chlorophyll begins to degrade.

Photosynthetic life then has a temperature tolerance that encompasses most worlds we would consider “habitable”, i.e. able to support liquid water on the surface (average surface temperature of  $0^{\circ} < T < 100^{\circ}$  assuming  $P=1$  atm).

For a more-or-less Earth-like planet in the habitable zone of another star, the spectral and flux requirements for photosynthesis may vary substantially with the changes in the primary energy source (the star) and its characteristics.

Photosynthetic pigments on Earth have been shown to absorb in the wavelength ranges of 330-900 nm and 1,000-1,100 nm (Schreer, 2003) with oxygenic photosynthesis limited to  $\sim 400$ -730 nm. No known photosynthesizer can absorb wavelengths longer than  $\sim 1,110$  nm despite 30% of the solar irradiance being within this range (Blankenship, 2002). Kiang et al. (Paper II), referencing the work of Wolencroft and Raven (2002), suggest that there is no theoretical upper wavelength constraint if more photons are used in each photosystem and photosystems are chained together (i.e. a multiple Z-scheme). However, a possible constraint may come when lower energy photons (large wavelengths) induce only vibrational transitions in molecules instead of the electronic transitions that are necessary for the energy cascade process.

Before we discuss upper and lower flux limits for photosynthesis, we first state an important point made by Kiang et al. in both Paper I and Paper II: photosynthesis, because it is a process that requires light *quanta* to drive redox reactions, is fundamentally dependent on *photon* flux density rather than energy flux density. This is crucial because the wavelength of peak energy intensity of a black body is different than the wavelength of peak photon intensity (this will be discussed in the next section). For example, the Sun’s peak energy flux density at the top of Earth’s atmosphere is 450 nm while its peak photon flux density occurs at 572-584 nm (Segura et al, 2005). The lower photon flux limit is determined by the balance between the productive capacity of photosynthesis and the needs of respiration while the upper limit may be set by resource limits (e.g. nutrients) and resilience against photo-oxidation damage (Kiang et al., Paper I). Kiang et al. (Paper II), reviewing the literature, quote lowest observed photon flux requirement of  $1.8 \times 10^{18}$  photons  $\text{m}^{-2} \text{s}^{-1}$  ( $0.7 \text{ W m}^{-2}$ ) for green plants in the PAR (Nobel, 1999) and  $1.8$ - $6.0 \times 10^{15}$  photons  $\text{m}^{-2} \text{s}^{-1}$  ( $\sim 0.002 \text{ W m}^{-2}$ ) for a brown sulfur bacterium living at a depth of 80m in the Black Sea (Overmann et al., 1992). Wolstencroft and Raven (2002) conjecture a theoretical upper photon flux tolerance limit (in Earth’s PAR) of  $3.6$ - $5.4 \times 10^{21}$  photons  $\text{m}^{-2} \text{s}^{-1}$  (compared to a typical Earth surface flux of  $1.2 \times 10^{21}$  photons  $\text{m}^{-2} \text{s}^{-1}$ ). Photosynthetic organisms may survive higher surface fluxes by living under water, which will attenuate the photon flux.

The flux of high-energy photons above the PAR must also be considered, as UV light is damaging to DNA and the subsequent production of oxygen radicals can inflict further damage on the cell. Damage to plants has been measured from UVB radiation at doses of  $2.6$ - $2.8 \times 10^{17}$  photons  $\text{m}^{-2} \text{s}^{-1}$  (Kakani et al, 2003). Earth’s maximum UVB flux is  $1.8$ - $2.8 \times 10^{18}$  photons  $\text{m}^{-2} \text{s}^{-1}$ , but averages an order of magnitude less (Kiang et al., Paper I). Life on Earth has shown some facility in adapting to photo-oxidative conditions. The non-photosynthesizer *D. radiodurans* uses maganese(II) to mitigate the effects of radical oxygen species and has remarkable resistance to DNA and cell damage by ionizing radiation (see Cox and

Battista, 2005). A photosynthesizer that evolved on a planet with a much higher UV flux than Earth may have incorporated these same adaptations, thus pushing up the UV tolerance range.

## Photosynthesis on Other Worlds

### *Spectral classes of stars and their habitable zones*

Stars can be categorized into seven major spectral classes O,B,A,F,G,K, and M starting with the largest, most luminous and hottest stars and trending towards the smaller, dimmer, and cooler stars. In the contemporary Morgan-Keenan system additional information is added to the spectrum letter with a number between 0 and 9 that indicates the range between the two star classes. Finally, Roman numerals can be added that describe the widths of important absorption lines in the stellar spectrum. These numerals indicate the size of the star and by implication its luminosity. Stars in the class V are main sequence stars i.e. stars fusing hydrogen in their cores. In this system, the Sun is a G2V.

Looking for inhabited planets, we are interested in main sequence stars with evolutionary lifetimes long enough to support the evolution of complex life, e.g. more than a billion years. Table 1 reproduced from Karttunen et al. lists the stellar lifetimes for different spectral classes of stars. It is evident that the stellar spectral classes with lifetimes comparable to the Sun are the F, G, K, and M spectral classes. Note that due to the initial mass function (Salpeter, 1955) and shorter lifetime the population of high-mass stars is much smaller than that of low-mass stars in our Galaxy.

**Table 1.** Estimated Stellar Lifetimes

Mass (solar masses)	Main Sequence Spectral Type ( $10^6$ yrs)	Main Sequence Lifetime ( $10^6$ yrs)
30	O5	4.9
15	B0	10
9	B2	22
5	B5	68
3	A0	240
1.5	F2	2,000
1.0	G2	10,000
0.5	M0	30,000
0.1	M7	$10^7$

The habitable zone is generally defined as the range of semi-major axes around a star in which a planet can sustain liquid water on its surface (Hart, 1978; Kasting et al., 1988). This is dependent on the luminosity of the parent star, the spectral distribution of the star's energy, and the atmospheric characteristics and status of geological activity of the planet. As stars evolve during the main sequence, their luminosity increases. The continuously habitable zone (CHZ) is defined as the region of orbital distances where a planet can maintain liquid water throughout the bulk of the parent star's main sequence lifetime. Kasting et al. (1993) find the CHZ for Earth to be between 0.95 and 1.37 AU. Using

different stellar input flux and one dimensional climate models, they find the habitable zones for F stars are larger and occur at larger distances from the star while K and M habitable zones are smaller and closer to their stars. Their conservative estimates for the sizes of the habitable zones are 0.25-0.35 AU for M0 stars and 1.85 to 2.70 AU for F0 stars.

### Photon spectra of other stars

In most cases, stellar spectra can be approximated as blackbodies with a spectrum determined by the Stefan-Boltzmann Law (3), which is derived by integrating the Planck function (4) over all frequencies (or wavelengths in the case of the form of the equation below).

$$j^*(T) = \frac{2\pi^5 k^4}{15c^2 h^3} T^4 = \sigma T^4 \quad (3)$$

$$I(\lambda, T) = \frac{2hc^2}{\lambda^5} \frac{1}{e^{\frac{hc}{\lambda kT}} - 1} \quad (4)$$

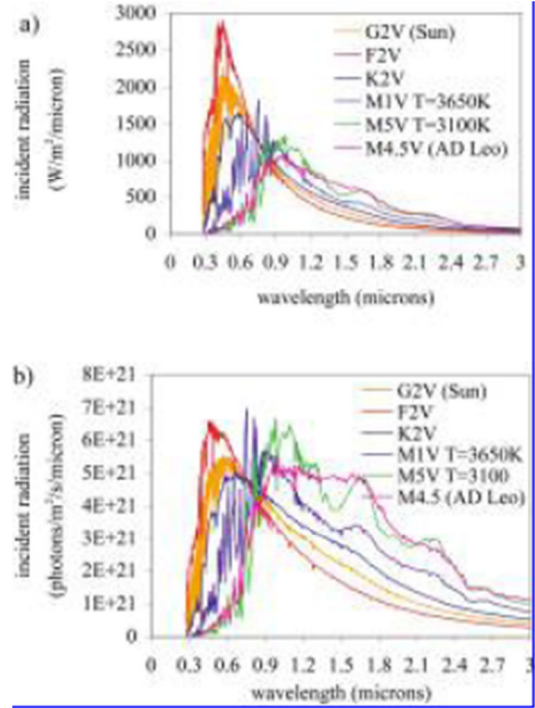
In the above equations,  $j^*$  is the energy flux density,  $\sigma$  is the Stefan-Boltzmann constant,  $T$  is the effective blackbody temperature,  $h$  is Planck's Constant,  $k$  is the Boltzmann Constant,  $c$  is the speed of light,  $\lambda$  is the wavelength, and  $I$  is the specific intensity.

The spectrum of a star can then be approximated as a function of the temperature of the stellar photosphere. For cooler M stars, however, this approximation is complicated by numerous molecular absorption bands in the star's spectrum (the star's lower temperature allows molecules to survive in the photosphere without being photo-dissociated). Young M stars are also known to have X-ray flares whose effects on planetary life must be considered.

As we noted previously, photosynthesis depends on photon flux, not energy flux, so it's more relevant to consider stellar spectra in terms of photon intensity instead of energy intensity. The Planck function can be modified by dividing it by  $hc/\lambda$  (individual photon energy) to obtain a photon intensity function (5) where  $n^*(\lambda, T)$  is the specific photon intensity.

$$n^*(\lambda, T) = \frac{I(\lambda, T)}{hc/\lambda} = \left( \frac{2hc^2}{\lambda^5} \frac{1}{e^{\frac{hc}{\lambda kT}} - 1} \right) \left( \frac{\lambda}{hc} \right) = \frac{2c}{\lambda^4} \frac{1}{e^{\frac{hc}{\lambda kT}} - 1} \quad (5)$$

In Figure 2, we reproduce spectra from Segura et al. (2003, 2005) that show the radiation flux at the top of the atmospheres of Earth-like planets that have average surface temperatures of 288 K in the CHZ zones of F2V, K2V, quiescent M5V and M1V stars and the active M4.5V star AD Leo. In addition, the real solar spectrum at the top of Earth's atmosphere is shown. Figure 2a shows the spectra in terms of



**Fig 2** – Top-of-atmosphere incident flux spectra in terms of a) energy and b) photons for considered parent stars (Segura et al., 2003, 2005; Kiang et al., Paper II)

The wavelength of peak photon flux density for each model planet is listed below in Table 2 (Kiang et al. Paper II).

**Table 2** – Wavelength of Peak Photon Flux

Parent Star Spectral Type	Wavelength of Peak Photon Flux (nm)
Sun (G2V)	685
F2V	451
K2V	667
M1V	754
M5V	1045

The peak wavelength for photon flux on Earth is at 685 nm, close to the peak absorbance values of photosystems I (700 nm) and II (680 nm). This at least partially explains why chlorophyll pigments are green despite the peak energy flux from the Sun being in this spectral region. Kiang et al. (Paper II) argue that extrasolar photosynthetic pigments would have their peak absorbance near the values given in Table 2. A discussion of the implications for the color of plants living under alien Suns can be found in the popular science article Kiang et al. (2008).

Kiang et al. (Paper II) calculate the average (cloud free) photon flux densities for several spectral regions (potential PARs) on the modeled planets with 1 PAL O<sub>2</sub> and an anoxygenic scenario of 10<sup>-5</sup> PAL O<sub>2</sub> for the M5V star. Additionally, they calculate the photon flux densities at 5 cm and 100 cm under water for the planet orbiting the M5V star to account for the possibility that flares will render surface life implausible. Table 3 below shows their results.

**Table 3** – Incident photon flux densities at the Surface and Under Water (Kiang et al., Paper II)

	Photon flux density ( $\times 10^{20}$ photon/m <sup>2</sup> /s)								
	F2V (1 PAL)	G2V (Sun/Earth)	K2V (1 PAL)	M1V (1 PAL)	M4.5V (1 PAL)	M5V (O <sub>2</sub> $\times 10^{-5}$ )		M5V Under water (O <sub>2</sub> $\times 10^{-5}$ )	
						1 PAL	5 cm	100 cm	
a. Solar noon									
UVB 280–315 nm	0.049	0.018	0.015	0.001	0.000	0.000	0.000	—	—
UVA 315–400 nm	2.319	0.871	0.588	0.095	0.021	0.016	0.016	—	—
PAR									
400–700 nm	16.4	11.0	11.5	6.1	1.8	1.5	1.5	1.4	1.1
400–1,100 nm	29.8	23.8	26.3	23.2	16.1	17.3	16.9	9.9	1.5
400–1,400 nm	34.0	28.6	32.1	29.3	23.7	25.7	24.9	10.2	1.5
400–1,800 nm	37.9	33.7	38.9	36.4	34.2	35.3	34.3	10.2	1.5
400–2,500 nm	40.5	36.9	43.3	40.2	40.0	40.1	38.4	10.2	1.5
Peak photon flux	450.8	668.5	666.6	753.5	1,045.1	1,042.8	1,042.8	1,073.2	1,073.2
Wavelength range (nm)	451.0	685.5	667.8	754.3	1,045.9	1,043.6	1,043.6	1,075.7	1,075.7
b. Illuminated face average									
UVB 280–315 nm	0.006	0.017	0.003	0.000	0.000	0.000	0.000	—	—
UVA 315–400 nm	0.940	0.518	0.241	0.040	0.009	0.007	0.007	—	—
PAR									
400–700 nm	7.5	6.3	5.4	2.9	0.9	0.7	0.7	0.7	0.5
400–1,100 nm	13.8	12.4	12.3	10.8	7.4	7.8	7.8	4.7	0.7
400–1,400 nm	15.6	14.2	14.8	13.2	10.6	11.0	11.0	4.8	0.7
400–1,800 nm	17.4	16.4	17.9	16.2	15.0	15.0	15.0	4.8	0.7
400–2,500 nm	18.5	17.6	19.8	17.7	17.3	16.5	16.5	4.8	0.7

In b, average fluxes are approximated by the photon flux at a solar zenith angle of 60° from vertical.



Table 3 demonstrates that all theoretical PAR bands on each planet have high enough photon flux intensities to support both the brown sulfur bacteria mentioned earlier ( $1.8 \times 10^{15}$  photons  $\text{m}^{-2} \text{s}^{-1}$ ) and green vascular planets ( $1.8 \times 10^{18}$  photons  $\text{m}^{-2} \text{s}^{-1}$ ). Photosynthesis appears to be very feasible on alien worlds.

#### *Estimates of photosynthetic productivity*

Photon flux levels are high enough on each of the planets we've considered to support photosynthesis not only for efficient unicellular organism, but also for more complex green land plants. A natural question is how globally productive a biosphere on one of these worlds could be, because the detectability of photosynthetic signatures (for example, seasonal fluxes of  $\text{CO}_2$ ) is dependent on the net productivity of ocean and land organisms (Kiang et al, Paper II).

In Table 4, Kiang et al. (Paper II) estimate the global productivity of each planet (in global  $\text{CO}_2$  flux) by assuming life is photon-limited (as opposed to nutrient-limited) and integrating photon flux over all solar angles, including clouds, and assuming an ocean/land ratio similar to that of the Earth. They also calculate productivity if the alien photosynthesizers use different numbers of photons for each reaction in their photosystem analogs.

**Table 4** – Time and disk-average incident photon flux and photosynthetic productivity estimates assuming a photon-limited biosphere under plausible quantum requirement scenarios (Kiang et al., Paper II)

	F2V (1 PAL)	G2V (Sun/Earth)	K2V (1 PAL)	M1V (1 PAL)	M4.5V (1 PAL)	M5V	
						(O <sub>2</sub> × 10 <sup>-5</sup> )	1 PAL
Time- and disk-averaged surface incident radiation (× 10 <sup>20</sup> photons/m <sup>2</sup> /s)							
UVB 280–315 nm	0.002	0.006	0.001	0.000	0.000	0.000	0.000
UVA 315–400 nm	0.357	0.197	0.092	0.015	0.003	0.003	0.003
PAR							
400–700 nm	2.8	2.4	2.0	1.1	0.3	0.3	0.3
400–1,100 nm	5.2	4.7	4.7	4.1	2.8	3.0	3.0
400–1,400 nm	5.9	5.4	5.6	5.0	4.0	4.2	4.2
400–1,800 nm	6.6	6.2	6.8	6.2	5.7	5.7	5.7
400–2,500 nm	7.0	6.7	7.5	6.7	6.6	6.3	6.3
GPP with Earth-like quantum requirements (× 10 <sup>18</sup> quanta/m <sup>2</sup> /s)							
PAR							
400–700 nm	0.85	<b>0.72</b>	0.61	0.33	0.10	0.08	0.08
400–1,100 nm	1.56	1.40	1.39	1.22	0.84	0.88	0.88
400–1,400 nm	1.76	1.60	1.68	1.50	1.20	1.25	1.25
400–1,800 nm	1.87	1.74	1.86	1.68	1.46	1.48	1.48
400–2,500 nm	1.94	1.81	1.97	1.76	1.59	1.57	1.57
GPP at 1.5×, 2×, 3×, and 4× quantum requirements (× 10 <sup>18</sup> quanta/m <sup>2</sup> /s)							
PAR							
400–1,100 nm	1.04	—	0.93	0.81	0.56	0.59	0.59
400–1,400 nm	0.88	—	0.84	0.75	0.60	0.62	0.62
400–1,800 nm	0.62	—	0.62	0.56	0.49	0.49	0.49
400–2,500 nm	0.48	—	0.49	0.44	0.40	0.39	0.39

Assuming Earth-like quantum requirements for the biochemical redox reactions and similar PARs, alien photosynthetic biospheres can be ~11% (for M5V stars) to ~118% (for F2V stars) as productive as Earth's. This number can increase substantially for wider PARs, but will decrease for larger quantum requirements. See Kiang et al. Paper II for further discussion.

## Summary and Conclusion

We have reviewed the literature, including the processes and limits of photosynthesis, and concluded that photosynthesis on extrasolar planets in the habitable zone of stars with differing spectral type is indeed plausible assuming environmental and nutrient requirements are met. We presented the work of Kiang et al. (Paper I, Paper II) and find that the potential global productivity of photosynthetic biospheres on other worlds does not differ markedly from the Earth's and can indeed exceed it. The detection of these biospheres will be predicated on their net productivity. Two factors contributing to an alien biosphere's detection will 1) be its effect to the reflectance spectrum of its planet and 2) the modification of its atmosphere with biogenic gases such as O<sub>2</sub> and CH<sub>4</sub>. Further discussion on the detection of biosignatures on extrasolar planets can be found in the Kiang et al. and the references therein.

## References

- Anderson, A. W., Nordon, H. C., Cain, R. F., Parrish, G. & Duggan, D. Studies on a radio-resistant micrococcus. I. Isolation, morphology, cultural characteristics, and resistance to  $\gamma$  radiation. *Food Technol.* 10, 575–578 (1956)
- Blakenship, R.E. (2002) *Molecular Mechanisms of Photosynthesis*, Blackwell Science, Oxford, UK.
- Blakenship, R.E. and Prince, R.C. (1985) Textbook errors: Excited-state redox Potentials and the Z scheme of photosynthesis. *Trends Biochem. Sci.* 10(10), 382-3
- Catling, D.C., Zahnle, K.J., and McKay, C.P. (2001) Biogenic methane, hydrogen escape, and the irreversible oxidation of early Earth. *Science* 293(5531), 839-843.
- Cox, M.M., Battista, J.R. (2005) *Deinococcus radiodurans* – the consummate survivor. *Nature*, 3, 882-892
- Crisp, D. (1997) Absorption of sunlight by water vapor in cloudy conditions: A partial explanation for the cloud absorption anomaly. *Geophys. Res. Lett.* 24, 571-574
- Grovindjee (1999) On the requirement of minimum number of four versus eight quanta of light for the evolution of one molecule of oxygen in photosynthesis: a historical note. *Photosynthesis Res.* 59(23), 249-254
- Hart, M.H. (1978) The evolution of the atmosphere of the Earth. *Icarus* 33(1), 23-39.
- Joliot, P. and Joliot, A. (2002) Cyclic electron transfer in plant leaf. *Plant Biol.* 99(15), 10209-10214
- Kakani, V.G., Reddy, K.R., Zhao, D., and Sailaja, K. (2003) Field crop responses to ultraviolet-B radiation: a review. *Agric. Forest Meteorol.* 120(1-4), 191-218
- Karttunen, H., Kroger, P., Oja, H., Poutanen, M., Donner, K.J. (1994) *Fundamental Astronomy*. Springer.
- Kasting, J.F., Whitmire, D.P., and Reynolds, R.T. (1993) Habitable zones around main sequence stars, *Icarus* 101(1-3), 108-128
- Kasting, J. F., Toon, O.B., and Pollack, J.B. (1998) how climate evolved on the terrestrial planets. *Sci Am.* 256, 90-97
- Ke, B. (2001) *Advances in Photosynthesis, Vol. 10: Photosynthesis: Photobiochemistry and Photobiophysics*, Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Kiang, N.Y., Siefert, J., Govindjee, and Blakenship, R.E. (2007) Spectral signatures of photosynthesis. I. Review of Earth organisms. *Astrobiology* 7(1), 222-251

- Kiang, N.Y., Segura, A., Tinetti, G., Govindjee, Blackenship, R.E., Cohen, M., Siefert, J., Crisp, D., Meadows, V. (2007) Spectral signatures of photosynthesis. II. Coevolution with other stars and the atmosphere on extrasolar worlds. *Astrobiology* 7(1), 252-274
- Meadows, V.S. and Crisp, D. (1996) Ground-based near-infrared observations of the Venus nightside: the thermal structure and water abundance near the surface. *J. Geophys. Res.* 101, 4595-4622
- Miller, S.R., Wingard, C.E., and Catenholz, R.W. (1998) Effects of visible light and UV radiation on photosynthesis in a population of a hot spring cyanobacterium, a *Synechococcus* sp., subjected to high-temperature stress. *Appl. Environ. Microbiol.* 64(10), 3893-3899
- Overmann, J., Cypioka, H., and Pfennig, N. (1992) An extremely low-light-adapted phototrophic sulfur bacterium from the Black Sea. *Limnol. Oceanogr.* 37(1), 150-155
- Rothschild, L.J., Mancinelli, R.L. (2001) Life in extreme environments. *Nature* 409(2), 1092-1101
- Salpeter, E., (1955) The luminosity function and stellar evolution. *Apj* 121, 161
- Schreer, H. (2003) The pigments. In *Advances in Photosynthesis and Respiration, Vol. 13: Light-Harvesting Antennas in Photosynthesis*, edited by B.R. Green and W.W. Parson, Dordrecht, The Netherlands, Kluwer Academic Publishers, pp. 29-81.
- Segura, A., Krelove, K., Kasting, J.F., Sommerlatt, D., Meadows, V., Crisp, D., Cohen, M., and Mlawer, E. (2003) Ozone concentrations and ultraviolet fluxes on Earth-like planets around other stars. *Astrobiology* 3(4), 689-708.
- Seguara, A., Kasting, J.F., Meadows, V., Cohen, M., Scalo, J., Crisp, D., Butler, R.A.H, and Tinetti, G. (2005) Biosignatures from Earth-like planets around M dwarfs. *Astrobiology* 5(6), 706-725.
- Tinetti, G. Meadows, V.S., Crisp, D. Fong, W., Fishbein, E., Turnbull, M., and Bibring, J.P. (2006) Detectability of planetary characteristics in disk-averaged spectra. I: The Earth model. *Astrobiology* 6(1), 34-47
- Wolstencroft, R.D. and Raven, J.A. (2002) Photosynthesis: likelihood of occurrence and possibility of detection on Earth-like planets. *Icarus* 157(2), 535-548.