

Survivability of Photosynthetic Bacteria in Non-Terrestrial Light

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Abstract

We explore whether a basic process of Life on Earth. Bacterial photosynthesis can in principle survive under alien light conditions defined by abnormal temporal correlations in the incident photon absorption times. Though unlike radiation from our own Sun, such extreme photon statistics have already been demonstrated under laboratory conditions and hence are allowed by the laws of physics. Our analysis exploits a detailed membrane model of the bacterial photosynthetic system *Rs. Photometricum* using state-of-the-art empirical inputs. Our results show that a broad range of extreme light conditions including those far beyond terrestrial sunlight do indeed support the metabolic needs of the terrestrial bacteria.

Keywords: Non-terrestrial; Photosynthetic; Sphaeroids; Absorption rates; Photon arrival model

Introduction

It is well-known that photosynthesis is responsible for most of the metabolic processes underlying Life on Earth [1-12]. Despite the many hypotheses about the origin of photosynthesis, there is little certainty about its earliest origin. Analyses of meteorites reveal a rich organic composition [13-15] which has led to speculation that some life forms could have resulted from the chemical development of organic material provided from outer space [16]. This raises the question as to whether Earth-like life forms might have developed elsewhere and as a corollary, whether existing Earth-like lifeforms would survive near more alien light sources. In this paper we carry out this examination of in-principle survivability by considering a subset of possible alien light sources where the temporal correlations are qualitatively different from those experienced on Earth due to the Sun. Though the incident light properties that we consider here are purposely very different from our own Sun, such extreme photon statistics have already been demonstrated under laboratory conditions and are allowed by the laws of physics – therefore it is plausible that they exist somewhere in the Universe.

Bacterial photosynthesis is arguably the oldest form of photosynthetic life [13,17]. Its structural simplicity, as compared with higher organisms like algae or plants [2], makes it an ideal focus for research. There are several studies on bacterial photosynthesis that go into a deep description of the structure, organization and dynamics of the photosynthetic apparatus [18]. During the last decade, experimentalists have been devoted to the study of the membrane structure through Atomic Force Microscopy (AFM) imaging, revealing a rich organization of the photosynthetic apparatus. Specifically, [1] reported a relationship in *Rsp. Photometricum* between the membrane stoichiometry and the light intensity during the growing stage. This link has now been confirmed on other types of bacterial systems such as *Rps. Palustris* [19] and *Rb. sphaeroides* [20].

This paper analyzes how temporal correlations in the photon absorption influence the survivability of photosynthetic bacteria. Our theoretical model was presented and validated [21,22] where it was shown to capture and successfully explain the remarkable chromatic adaptation of [1] in terms of a dynamic interplay between excitation kinetics and the RC cycling. Reference [23] provided a preliminary exploration of purely temporal correlations in the incident photon

absorption; however we present here a fuller calculation using updated input parameters and more sophisticated computer code. Following [23] we focus on two statistical properties to characterize the output of quinol production $\gamma(t)$ from the reaction centers. Our specific focus is the burstiness B and memory M of this time-series $\gamma(t)$. A Poisson process corresponds to $(M, B) \approx (0, 0)$ which is the approximate result expected for photosynthetic organisms which live (and hence survive) on Earth. Values of B and M that deviate significantly from $(0, 0)$ correspond to a quinol production that is very different from that experienced by the organism on Earth, and hence would likely kill it [23]. Such extreme value statistics have recently been observed in phenomena such as optical Rogue waves [24] and coherent anti-Stokes Raman scattering in silicon [25]. These sources emerge from processes that are allowed by the laws of physics and hence plausibly occur somewhere in the Universe. They are not restricted to a (M, B) value close to zero and hence open new roads of research. As a note, we do not here consider the additional complication of extremes in intensity and spectral composition since that just adds additional level of complexity to the incident light. The physical processes that generate extreme photon statistics do not a priori require extreme intensities or spectral compositions.

Photosynthetic Membrane Model

In purple bacteria (Figure 1) the photon absorption is accomplished by light harvesting complexes (LHC) that are spatially distributed on the cytoplasmic membrane [26]. The photo-excitation is then transferred to the photosynthetic reaction center (RC) where a charge separation process is initiated when charge carriers are available [18]. Our model uses a stochastic approach to the classical rate equations for a large number of LHC (≈ 400). It accounts for photon absorption,

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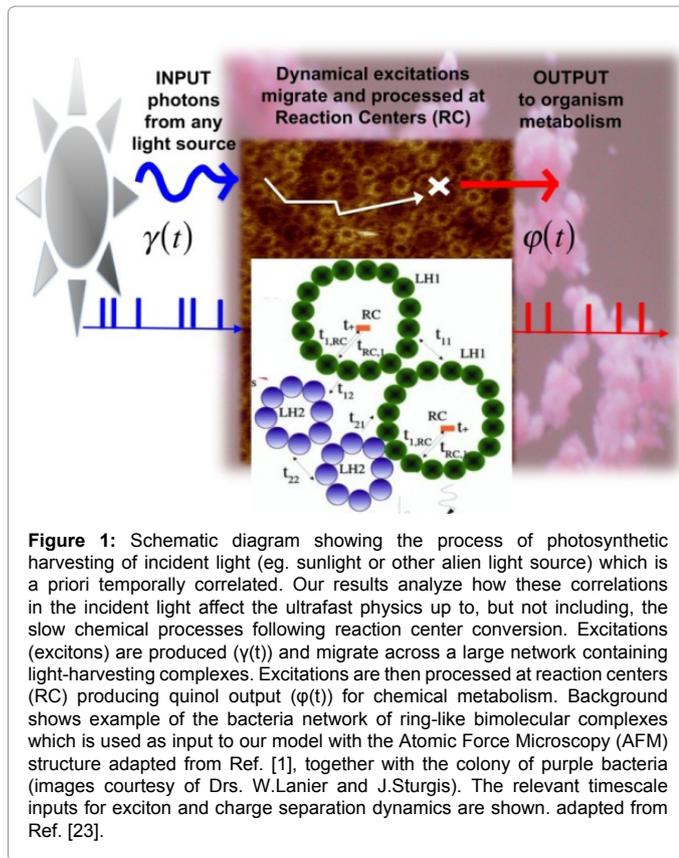


photo-excitation transfer and RC cycling for a given architecture and light statistics, as well as photon loss through other processes. At each time-step ($\delta t \approx 0.025\text{ps}$), incoming photons are being absorbed by the antenna complexes LH1 and LH2 with absorption rate $\gamma_A = I(\gamma_1 N_1 + \gamma_2 N_2)$, where $\gamma_{1(2)}$ and $N_{1(2)}$ are the absorption rates [27] and number of LH1(2) complexes, respectively. At the same time, present photo-excitations diffuse throughout the membrane in search for an open RC according to transfer rates resulting from experiments [28]. Some of these excitations will be dissipated through fluorescence or internal conversion at an assumed constant rate γ_D [27]. Meanwhile, closed RCs are processing the excitations that have already been received. Once an open RC has received two photo-excitations, it is set closed and no other photo-excitation is allowed to enter. After a time τ has elapsed from the moment in which the second photo-excitation has entered, the RC is set open and the cycle starts from the beginning. This open/close mechanism accounts for the time where two electrons produce quinol ($Q_B H_2$) before it undocks and a new quinone (QB) substitutes it.

This process lasts a few milliseconds and has shown to be key in order to explain the chromatic adaptation of the membrane stoichiometry (ratio of LH2 to LH1) under different light intensity conditions [21,22].

Transfer rate measures from pump-probe experiments agree with generalized Forster calculated rates [28], assuming intra-complex delocalization. LH2→LH2 transfer has been given as $t_{22}=10\text{ps}$ [28], while LH2→LH1 transfer has been measured for *R. Sphaeroides* as $t_{21}=3.3\text{ps}$ [29]. Back-transfer LH1→LH2 is approximately $t_{12}=15.5\text{ps}$ while the LH1→LH1 mean transfer time t_{11} has been calculated using a generalized Forster interaction [6] as 20 ps. Second and third lowest

exciton lying states cause LH1→RC transfer due to ring symmetry breaking [30], consistent with a transfer time of 35-37 ps found experimentally at 77 K [31,32]. As proposed by Grondelle et al. [33], increased spectral overlap at room temperature improves the transfer time to $t_{1,RC}=25$ ps. The back-transfer from an RC's fully populated lowest exciton state to higher-lying LH1 states occurs in a calculated time of $t_{RC,1}=8.1$ ps [30], which is close to the experimentally measured 7-9 ps estimated from decay kinetics after RC excitation [34]. The subsequent passage through the RC complex depends on whether a charge carriers is available (i.e. the RC is in an open state), to occur within $t_+ = 3\text{ps}$.

Photon arrival model

We classify the temporal characteristics of both the input photon arrival and the quinol output using the two statistical measures B and M, which were introduced in Ref. [26] and employed in Ref. [23]. The burstiness B measures how far a distribution is from that emerging out of a Poisson process, i.e.,

$$B \equiv (\sigma_t / m_t - 1) / (\sigma_t / m_t + 1)$$

Where m_t and σ_t are the mean and standard deviation of the inter event time series, respectively. The memory M between consecutive intervals is defined as:

$$M \equiv (1 / (n_t - 1)) \sum_{i=1}^{n_t-1} (t_i - m_t)(t_{i+1} - m_t) / \sigma_t \sigma_2$$

Where n_t is the number of intervals and $m_{1(2)}$ and $\sigma_{1(2)}$ are the mean and standard deviation of the t_i (t_{i+1})'s respectively ($i=1, \dots, n_t-1$) [26]. These values by definition lie between -1 and 1. Other non-Poisson processes may be characterized by B and M values away from the origin.

Though certain inputs may have values of B and M that are very different from zero, and hence very unlike the experience on Earth, the quinol production output may end up lying very close to $(B, M) \approx (0, 0)$. This arises because of the non-linearity of the membrane processing of excitations (Figure 1) and signals potential survivability of the corresponding organism under these extreme alien light conditions.

Results and Discussion

Figure 2 shows an updated version of our preliminary results from Ref. [23]. It identifies the regions in the B – M space that fulfill the requirement of survivability. As an illustration, we have chosen the bunched (left) and power law (right) input for the photons being absorbed (Figure 1). The circles represent B – M values for the incident photon absorption time series (input), while the trajectory of the same color illustrates the quinol production output for different values of closed time τ . We assume that all (or a constant fraction) of the arriving photons get absorbed and hence that the time series of absorbed photons is statistically equivalent to that of the incident light. The gray region represents the forbidden values of B and M for this type of time series. The red region illustrates the region in the B – M plane where the output is bursty and therefore potentially damaging for the metabolism of the photosynthetic organism. The white region shows the region where the quinol production output resembles the one on Earth and therefore the survival of the bacteria. The time series are generated in such a way that they preserve the average intensity regardless of their inter-event statistics, hence preserving the temperature of the system. We point out that while the choice of the size of the survivability range (0.05) in Figure 2 can be varied, the important conclusions of our work do not change: namely that our results show that there is a highly nonlinear relationship between the input photon statistics and the output quinol

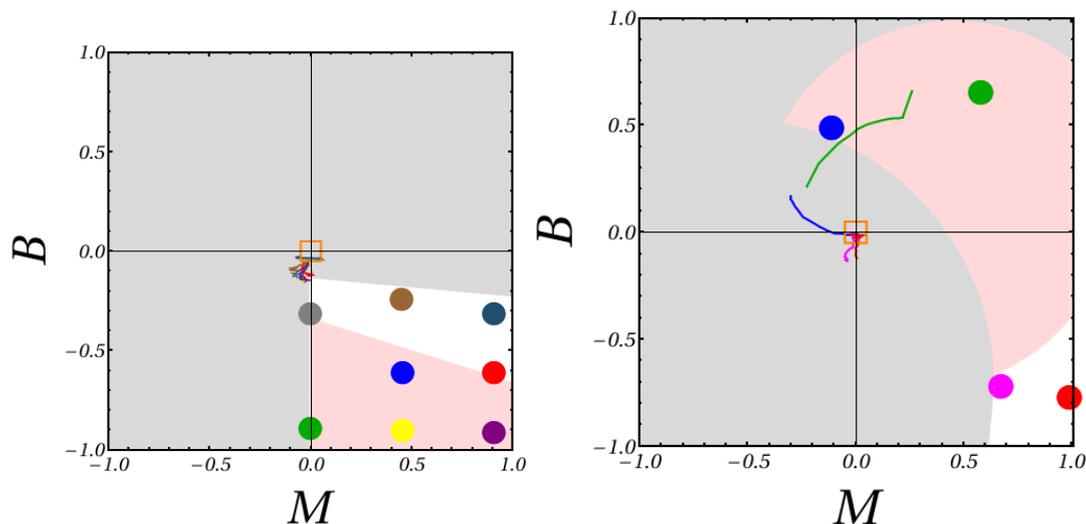


Figure 2: BM measurements for two types of photon arrival time series: bunched (left) and power law (right). The large circles are the BM values for the input while the trajectories represent the quinol production output for different values of RC closed time τ . The gray regions are forbidden for the specific input time series. The red region shows the values where the output for the organism is bursty and likely to be too toxic. The white region produces output trajectories close to zero within the margin of 0.05 (orange square), and therefore correspond to survival in principle, i.e. these are the regions of survivability.

production. This unexpected result highlights the importance of our in-principle study. Current dogma is that the more extreme the conditions, the less likely an organism's survival whereas our results show that the opposite can happen. Furthermore, though it may be true that certain bacteria under certain larger deviations from 0.05 might still survive thanks to specific details of their membrane metabolism, the principle remains the same: assuming that evolution has driven organisms to adapt to conditions on Earth, then a metabolism that is given the same quinol production rate as on Earth will be more likely to survive if all other factors are kept equal. We also stress that our model does indeed include the effect of other loss mechanisms. Since any such lost photons are not available for quinol production, we are not concerned with precisely how these photons are lost and hence simply use a state-of-the-art loss rate.

Our results in Figure 2 confirm that even though certain inputs of incident light may be very unlike that experienced by photosynthetic bacteria on Earth, their metabolic quinol production output may end up lying very close to that required for survival because of the non-linearity of the membrane processing of excitations (Figure 1). This means that they could potentially survive under these extreme alien light conditions. We hope our results encourage the experimental study of bacteria under such unusual light sources as characterized by their temporal correlations and hence enrich ongoing discussions in the field of astrobiology [35].

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