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Random Distribution of Bacterial GC Content under the Ultraviolet Radiation

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Abstract: *The study of the GC content pattern is important because it reflects the environment to which bacteria belong and provides insights into how bacteria evolve. Many studies have focused on the effect of environmental factors on the DNA on bacteria, and ultraviolet radiation (UVR) is one of the most widely investigated factors. Among many theories about the effect between UV radiation and genomic GC content, we studied a doubtful theory that had not been well refuted, proposed by Singer and Ames in 1970 on Science. They proposed the positive correlation between bacterial genomic GC content and UVR, mainly supported by their measurement of the GC content of bacteria living in environments with different different UVR and the analysis on the protective mechanisms of bacteria against UVR. The article written by Bak, Atkins and Mayer in 1972 refuted Singer and Ames' proposal by presenting exceptions of unicellular organisms that do not follow the correlation and proposed the theory that the distribution of GC content is not much affected by UVR, showing a random state. Restricted by contemporary technology and academic progress, the two articles both lack direct measurements of genome arrangement, and they do not explain the detailed mechanisms behind their theories. In this paper, the arrangement of thymine in bacteria is measured, and the result contradicts Singer and Ames' theory, agreeing with Bak, Atkins and Mayer's theory. The possible explanation of mechanisms is summarized behind, which further supports Bak, Atkins and Mayer's theory. In other words, we have more precisely assessed and refined an old debatable theory by using modern technology and academic achievements.*

Keywords: *Genomic GC content, Ultraviolet Radiation (UVR), Genome Analysis*

1. Introduction

The genomic base composition varies widely across species and among chromosomes[1]. Bacteria GC content ranges from 13% to 75% [2] and possesses significant differences in different parts of the gene sequence[3][4]. GC content is one of the important factors considered in systemic bacteriology: if the difference between two bacteria is lesser than 10% to 12%, they appear possible to be homologous[5]. The study about the pattern of the GC content is important because the pattern reflects the environment the bacteria belong and provides insights on how the bacteria evolve. For example, as one study showed, bacteria that survive in soils with a low carbon-nitrogen ratio tend to have lower GC content than those that survive in soils with a high carbon-nitrogen ratio[6]. The results of this study can help determine the environment in which bacteria live.

Many studies are devoted to the effect of environmental factors on GC content in bacteria, and ultraviolet radiation is one of the factors extensively investigated. Ultraviolet (UV) is an important constitution of the visible light, which is lights that have wavelength between 400nm~10nm in vacuum, and is commonly classified into UVA(400nm-320nm), UVB(320nm~280nm), and UVC(280~100nm). While UVC is mostly blocked by the atmosphere, UVA and UVB radiate widely across the earth's surface, with significant impacts on the survival and evolution of bacteria exposed to it. In 1877, Downs and Blunt firstly reported that sunlight radiation can sterilize bacteria in culture medias. In 1878, the sterilization effect of ultraviolet light was discovered. But it wasn't until 1960 that people finally found out the essence of UV sterilization. When radiated by UV light, bacteria's DNA absorbs the energy of UV photons, causing adjacent thymines in the DNA sequence to fuse and become thymine dimers. The formation of thymine dimers alters the helix structure of DNA and stops the process of forming new RNA at the dimer site, which disrupts the DNA replication and transcription[7]. On the other hand, the ultraviolet radiation can excite light-reacted molecules, which further become sterilizers for the destruction of other molecules or lead to the formation of reactive oxygen species (ROS)[8]. ROS can cause the damage to other molecules, including DNA and lipids.[9] UV-caused DNA damages

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are mainly the result of the formation of thymine dimers and ROS. In DNA damage caused by ROS, guanine is the most susceptible type of nucleotide to oxidative stress, because it has the lowest oxidation potential.[10] The replication of the guanine damaged by oxidative stress results in G to T mutations[11], and when oxidatively damaged guanines are not in the reference strand, their replication would cause the C to A mutation in the reference strand. In literatures, this type of mutation were denoted by G:C to T:A mutations or G to T transversions[11][12][13][14][15][16]. The UV radiation can cause the formation of ROS which cause the G to T transversion, so the UV can lead to the decrease of GC content.

Among many theories about the effect between UV radiation and genomic GC content, we investigated a questionable theory that had not been well refuted.

In 1970, 10 years after the discovery of the essence of bacterial sterilization, Singers and Ames had published their article on Science proposing a strong correlation between the amount of sunlight a bacterium is normally exposed to and its GC content, considering mainly the effect of the formation of thymine dimers on DNA GC content[17]. According to their theory, the high GC content means that less thymines are in the sequence, so there would be less possibility for the thymines being adjacent to each other, and the specific thymine damage caused by ultraviolet radiation can be more avoided. Thus, bacteria with high GC content tend to have evolutionary advantages, which create a strong evolutionary driving force toward high GC content under natural selection and would even overwhelm some weaker selective pressures, such as ionizing radiation and the effect of some alkylating chemicals. They looked at organisms that form aerial conidia or fruiting bodies that produce carotenoids, or have a habitat near the surface of water as exposing to high UV radiation, and they looked at organisms that are obligate anaerobes and internal parasites as exposed to low UV radiation. By this standard, they gave tens of examples of bacteria with high GC content and high exposure to sunlight, as well as bacteria with low GC content and low exposure to sunlight to support their theory. They found only two exceptions (Cytophaga and Saprospira) that are difficult to explain by their theory. They also considered three UV protection mechanisms in bacteria that may interfere with their theory, including UV screening by cytoplasmic material, DNA repair, and the evolution of the DNA base ratio. According to their analysis, bacteria would need pigments that account for 10% of their dry weight to absorb half of the incident UV radiation, and they found no report of a pigment at such a high concentration in bacteria. Also, they believed that no DNA repair would be sufficient to reduce UV damage to an evolutionary insignificant value, because even a small amount of omission that causes bacteria to die (10-10 per generation with one generation per day as they considered it) should be a significant selective disadvantage. They believed that the evolution of the DNA base ratio would be effective, because it would only reduce the amount of thymine in its DNA, which is relatively small sacrifice but can obtain a significant selective advantage. They measured the advantage of increasing GC content and explained it by the predominant state of thymine constituted dimers in UV photoproducts. The reduction of thymine content would decrease the possibility of the formation of most UV photoproducts. In addition, they demonstrated that the base ratio change of DNA can still proceed with the amino acid sequence the DNA code for remains unchanged. Finally, they admitted that the mechanism for the very low GC content of bacteria's DNA when they are not exposed to sunlight was still unclear, and they thought one possible explanation is that naturally occurring alkylating chemicals may attack the thymine and create the low GC content.

Another article written by Bak, Atkins and Mayer was published in 1972 on Science, which refuted Singer and Ames' discovery[18]. In this article, the authors reported many exceptions that Singer and Ames did not consider. They found tens of fastidious parasitic bacteria that have high GC content, which should have low GC content according to Singer and Ames' theories. Also, many pigmented and strictly aerobic bacteria, which are usually found near the water surface, have low GC content. The article also pointed out that some bacteria Singer and Ames considered highly exposed to sunlight do not necessarily meet their expectations, even if they are soil organisms. The article also considered eukaryotes, because their GC content distribution is broad and approaches bacteria. According to the study, many eukaryotes have similar habitats but very different GC content, which is also not consistent with Singer and Ames' theory. In the end, the article concluded that, from their views, they did not feel that the potential selective advantage currently envisaged can account for GC content in unicellular organisms.

The article hypothesized that the distribution of unicellular GC content is largely random under UV light. The conservation of certain DNA sequence was used to support this general statement. The article referred to ribosomal cistron coding as examples, and pointed out that some mechanisms may be responsible for the observed distribution that might be the low frequency of errors in the replication and repair system, which accounts for the low mutation rate. And they also considered the influence of

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naturally selected different mutation rates, caused by types of mutator genes. The second support was the existence of a random distribution of DNA GC base composition in bacteria that survive in the same habitats.

Restricted by contemporary technology and academic progress, the two articles specifically mentioned above lack direct measurement of the content of thymine dimers, which is affected not only by GC content but also by the arrangement of thymines. Moreover, their explanations of the mechanism leading to the low GC content in bacteria, the explanation of the mechanism of exception unicellular organisms, and the reason for the random composition of DNA GC bases are all limited to unclear guesses. We directly measured the content and arrangement of thymine in bacteria that Singer and Ames measured and analyzed their effect on the formation of thymine dimers and whether this supports Singer and Ames' theory or not. In this article, we will also give more detailed and supported explanations for the mechanisms of low GC content, light protection in exceptional unicellular organisms, and the theory of random GC base composition under UV radiation.

2. Method

A total of 35 DNA genomes were downloaded from the NCBI database[19]. From Singer and Ames' measurements, the mean of all species in each of the 30 genera of bacteria surviving under certain UV exposure conditions was calculated. We selected one species from each of the 30 genera for our measurement and obtained their genomes from NCBI, which are the 30 genomes of the total 35 genomes. The other 5 are all genomes of unicellular organisms that belong to one of the species of each of the 5 genera in the *Prochlorococcaceae* family.

The 30 genera of bacteria Singer and Ames measured were selected to verify their theory by measuring of double thymine content and the tendency to contribute double thymine of the genome arrangement. In order to control the genetic relationship, the 5 species belonging to the *Prochlorococcaceae* family were used to further verify the theory, in which the two subspecies of *Prochlorococcus marinus* have 97% genetic similarity, but survive in different UV exposure environments. *Prochlorococcus marinus subsp.marinus* (MIT9313) lives in the bottom of the euphotic layer where little light can reach, while *Prochlorococcus marinus subsp.pastoris*(MED4) lives in a bright layer where sufficient sunlight can be received for photosynthesis[20].

We designed a program to analyze the content of double thymine and the tendency of the arrangement to contribute to double thymine. The program would scan genome information from the last nucleotide to the first. Once it finds a thymine, it would evaluate whether the next nucleotide is also a thymine. If so, the two thymine would be noted as double thymine. Then the program would skip the next nucleotide and scan until it completes the entire genome scan and annotation. The content of double thymine is calculated as the percentage of the total amount of thymine that constitutes the double thymine and the total amount of nucleotide in the genome. Then the whole genome would be randomly shuffled. The content of the double thymine would be calculated again and contracted with the content before shuffling, and the result of subtraction would also be noted. The program is coded in Python (see Appendix A).

Thymine dimers can be formed with two adjacent thymine, so the amount of adjacent thymine largely and more directly, compared to GC content, reflects the possibility of formation of thymine dimers. Shuffling is used to randomize nucleotide arrangement, which we consider the origin of arrangement. If the same amount of nucleotides are used, but the genome arrangement makes less double thymine appear before shuffling, the genome arrangement can be seen to contribute to the possibility of less double thymine and dimer thymine formation. Conversely, if the arrangement made more double thymine before shuffling, then the genome arrangement can be seen contributing to the possibility of more double thymine and thymine dimer formation. A chart was used to collect the information we obtained.

3. Result

The results of the analysis of 30 genomes from NCBI were listed in Table 1. We summarized the results of the analysis of the 30 genomes from NCBI in pie charts in Figure 1, Figure 2, and Figure 3. Figure 2 shows that 68.18% of the total highlight (HL) genome arrangement contributes to higher double thymine content, which means that even surviving in a high UV radiation environment, HL genome arrangement still favors the formation of thymine dimers. Figure 1 shows that 12.50% of the

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total low light (LL) genome arrangement contributes to lower thymine content, meaning that arrangement negatively affects the formation of thymine dimers. However, according to Singer and Ames' theory, bacteria living in a high-light environment need to lower the possibility of thymine formation by altering its genomic sequence, and there is no need for bacteria living in a low-light environment to lower the possibility. The results shown in Figure 1 and Figure 2 contradict the theory. Figure 3 shows that in all genomes we measured, 53.33% of their sequence arrangements are not congruent with Singer and Ames' theory.

Figures 1 and 2 also show that there is a tendency to favor the formation of double thymine in both HL and LL groups. In HL group, 68.18% of the genomic arrangement lead to more double thymine, and in LL group, 87.5% of the genomic arrangement lead to more double thymine.

The results of the analysis of the 5 species that belonging to the Prochlorococcaceae family were listed in Table 2. Only two of the five species are consistent with Singer and Ames' theory. Not only the arrangement but also the AT content of prochlorococcus marinus subsp. pastoris(HL) is not congruent with Singer and Ames' theory, which is notable. The result shows that even when the genetic relationship was controlled, there appears no clear relationship between the UVR of the habitat and the thymine dimer content or GC distribution of the organisms.

In conclusion, our genomic analysis is mainly against Singer and Ames' theory and supports Bak, Atkins and Mayer's theory.

We measured the natural double thymine content and the randomly shuffled double thymine content of the 30 species noted on the left. The subtraction is equals to the natural double thymine content subtracting the randomly shuffled double thymine content. For the high-light species, if the subtraction is negative, it is congruent with Singer and Ames' theory. For the low-light species, if the subtraction is positive, it is congruent with Singer and Ames' theory.

Table 1: The results of the analysis of the 30 genomes from NCBI

Name of the species	Double thymine content (original)	Double thymine content (shuffled)	Subtraction	UV exposure	Congruent with the theory or not
Micrococcus porci(HL)	2.49947	3.2002	-0.70073	Highlight	congruent
Actinoplanes missouriensis 431(HL)	3.26852	3.71196	-0.44344	Highlight	congruent
Streptomyces avermitilis MA-4680 = NBRC 14893(HL)	3.348	3.7	-0.352	Highlight	congruent
Sphaerotilus sulfidivorans(HL)	3.504	3.95	-0.446	Highlight	congruent
Chondromyces crocatus(HL)	3.8845	4.264	-0.3795	Highlight	congruent
Myxococcus stipitatus DSM 14675(HL)	4.013	4.08	-0.067	Highlight	congruent
Prosthecomicrobium hirschii(HL)	4.384	4.163	0.221	Highlight	not congruent
Halobacterium salinarum(HL)	4.655	4.88	-0.225	Highlight	congruent
Caulobacter vibrioides NA1000(HL)	5.12186	4.58736	0.5345	Highlight	not congruent
Mycobacterium tuberculosis H37Rv(HL)	5.373	5.045	0.328	Highlight	not congruent
Xanthomonas euvesicatoria pv. alfalfae(HL)	5.88453	5.27038	0.61415	Highlight	not congruent
Rhodospirillum rubrum F11(HL)	6.18607	5.09351	1.09256	Highlight	not congruent
Rhizobium tropici CIAT 899(HL)	7.7	6.812	0.888	Highlight	not congruent
Corynebacterium kroppenstedtii DSM 44385(HL)	8.285	7.549	0.736	Highlight	not congruent
Chlorobium limicola DSM 245(HL)	10.882	9.564	1.318	Highlight	not congruent
Chromatium okenii(HL)	11.38637	9.04467	2.3417	Highlight	not congruent
Saprospira grandis str. Lewin(HL)	13.68575	11.35819	2.32756	Highlight	not congruent
Sarcina ventriculi(HL)	21.15032	20.59113	0.55919	Highlight	not congruent
Flavobacterium johnsoniae UW101(HL)	19.033	16.265	2.768	Highlight	not congruent
Cytophaga hutchinsonii ATCC 33406(HL)	15.809	14.254	1.555	Highlight	not congruent
Catenibacterium faecis(LL)	16.43061	16.48018	-0.04957	Lowlight	not congruent
Treponema phagedenis(LL)	16.7402	13.64149	3.09871	Lowlight	congruent
Wolbachia endosymbiont of Drosophila melanogaster(LL)	17.176	15.969	1.207	Lowlight	congruent
Fusobacterium nucleatum subsp. nucleatum ATCC 25586(LL)	20.883	19.386	1.497	Lowlight	congruent
Mycoplasma capricolum subsp. capricolum ATCC 27343(LL)	23.223	20.829	2.394	Lowlight	congruent
Bacteroides thetaiotaomicron(LL)	13.581	12.8	0.781	Lowlight	congruent
Chlamydia trachomatis DUW3CX(LL)	14.639	13.233	1.406	Lowlight	congruent

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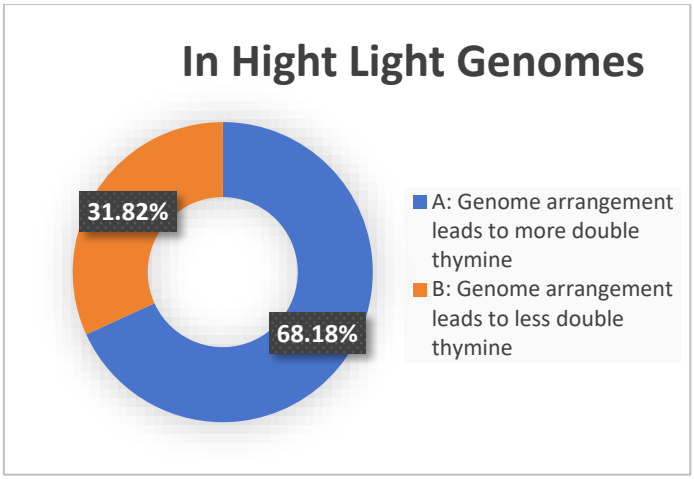

Figure 1

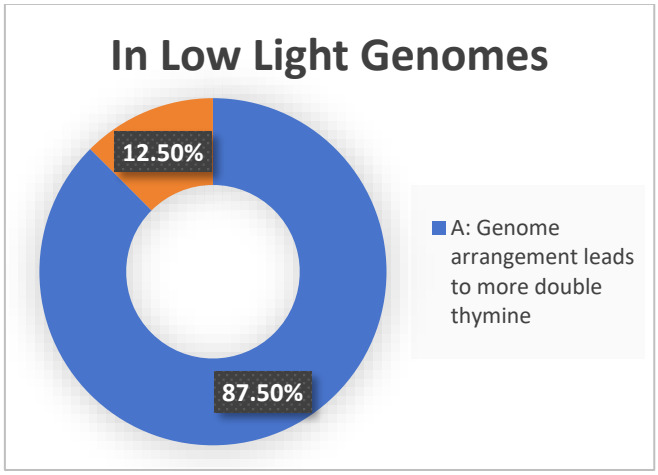

Figure 2

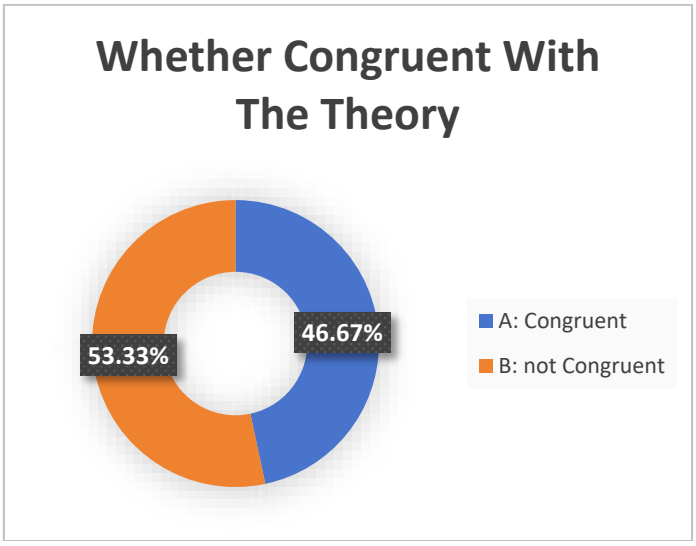

Figure 3

Figure 1 shows that 12.50% of the total low-light (LL) genome arrangement contributes to lower thymine content, meaning that arrangement negatively affects the formation of thymine dimers even in low-light environments. This is not needed according to Singer and Ames' theory.

Figure 2 shows that 68.18% of the total highlight (HL) genome arrangement contributes to higher double thymine content, which means that even surviving in a high UV radiation environment, HL

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genome arrangement still favors the formation of thymine dimers. This is the opposite to Singer and Ames' theory.

Figure 3 shows that in all genomes we measured, 53.33% of their sequence arrangements are not congruent with Singer and Ames' theory

We measured the natural double thymine content and the randomly shuffled double thymine content of the 5 species that belonging to the Prochlorococcaceae family. The subtraction is equals to the natural double thymine content subtracting the shuffled double thymine content. For the high-light species, if the subtraction is negative, it is congruent with Singer and Ames' theory. For the low-light species, if the subtraction is positive, it is congruent with Singer and Ames' theory.

Table 2: The results of the analysis of the 5 species belonging to the Prochlorococcaceae family.

Name of the species	Double thymine content(%) (Natural)	Double thymine content (%) (shuffled)	Subtraction
Cyanobium gracile(HL)	3.96001	4.16454	-0.2045
Cyanobium usitatum(HL)	6.69101	6.03824	0.653
Parasynechococcus marenigrum(HL)	7.48334	6.88732	0.596
Prochlorococcus marinus subsp. marinus(LL)	17.23894	15.20222	2.0367
Prochlorococcus marinus subsp. pastoris(HL)	20.063	17.943	2.12
Name of the species	UV exposure	AT content	Whether congruent with the theory
Cyanobium gracile(HL)	Highlight	31.292	Congruent
Cyanobium usitatum(HL)	Highlight	37.392	Arrangement not congruent
Parasynechococcus marenigrum(HL)	Highlight	40.587	Arrangement not congruent
Prochlorococcus marinus subsp. marinus(LL)	Lowlight	63.556	Congruent
Prochlorococcus marinus subsp. pastoris(HL)	Highlight	69.199	GC content and Arrangement not congruent

4. Discussion

Our results contradict Singer and Ames' theory, and some explanations can be given from many supported academic theories.

Singer and Ames' theory seems to be wrong, and Bak, Atkins and Mayer's suggestion that the distribution of unicellular GC content is largely random under UV light is more supported by our results. One possible explanation for this random state is that the evolutionary force towards high GC content is driven by the possible damage of thymine dimer counteracting the G-to-T reversal effect caused by formed ROS due to UV radiation. As suggested in the introduction, ROS formation is another major damage of UV radiation to bacteria. ROS can cause G to T traversion, and with more guanine transcribed to thymine, GC content would decrease while AT content would increase, which is an evolutionary driving force against the force created by thymine dimer damage. If the two forces interact, the unicellular GC content may increase or decrease, depending on the strength of the two forces. However, how strong each force is compared to the other needs further research. Singer and Ames mentioned that the evolutionary driving force created by the possible damage caused by thymine dimers is a strong driving force that can overwhelm many small driving forces. But the driving force created by ROS seems to be strong, because it not only reduces guanine but also provides more thymine.

Singer and Ames' theory was based on the idea that the evolutionary driving force created by the possible damage caused by thymine dimers is a strong force that can overwhelm many weak driving forces. However, there are still factors that may be out of control. *Prochlorococcus* is one of the genera we measured in our experiments, and the subspecies *Prochlorococcus marinus subsp. Pastoris*, which survive in HL, have not only GC content but also Genome arrangement, which is inconsistent with Singer and Ames' theory. We looked for the explanation of this exception, and we found that a recent study published on Nature in 2021 proved that *Prochlorococcus* is not, as people normally believed in default, majorly affected by natural selection but is instead mainly undergoing genetic drift[21]. According to this study, although prochlorococcus has wide distribution, different niches are occupied by different isolated populations with different metabolic characteristics. In different populations, no gene communication occurs and the state of isolation remains, resulting in a low level of genetic recombination, which makes natural selection to retain or eliminate the entire genome when certain genes are favored or not. This reduces the effective population size and neutral genetic diversity

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of *Prochlorococcus*, which reinforces the effect of genetic drift. When genetic drift plays a major role, but not natural selection, random mutation affects the genome more, but not the natural selection force driven by the damage caused by thymine dimers. Furthermore, as suggested in another article, genomic analysis of *Synechococcus*, *Cyanobium*, and *Prochlorococcus* shows that they possess up to five genes encoding different members of the photolyase or cryptochrome family[22]. When the 5 genes of *Synechococcus* are knocked out from them or endowed to the *Escherichia coli* that originally have no UV resistance, each are found to decrease the *Synechococcus'*s or increase *Escherichia coli*'s resistance to UV and their ability to survive in UV environment. Such a photolyase or cryptochrome can protect prokaryotes, including their DNA, which makes Singer and Ames' theory flawed. Factors such as dominant genetic drift, the presence of protective photolyase and cryptochrome may be the reason why a significant relationship between UV radiation and the distribution of cellular GC content is not found.

Not Singer and Ames' article nor Bak, Atkins and Mayer's article provided a clear explanation for the low GC content in bacteria. One possible explanation is the neutral theory suggested by this article published on PNAS in 1962[1]. Neutral theory holds that differences in GC content between organisms are due to genetic random mutation and drift. Cytosine methylation and deamination events occur rapidly in cells, causing cytosine and adenine to mispair. This would cause the cytosine to be replaced by thymine in the next round of replication. According to neutral theory, the overall trend of of DNA sequence mutation is with decreasing GC content and increasing AT content. Consequently, when not affected by other evolutionary drivers, bacteria tend to have low GC content, which may explain the existence of many bacteria with low GC content. Another possible theory to explain the mechanism, selection theory, believes that the difference in GC content is due to the mutual functions of factors such as organisms' environments and habits[23]. According to this theory, factors like the attack of naturally occurring alkylating chemicals to the thymines, as suggested by Singer and Ames, and the mistakes of DNA repair may be the result of the low GC contents in some bacteria.

Our work primarily contributed to a more direct assessment of the argument between the two articles in the 1970s about the effect of UVR on GC content by measuring the arrangement of genomic sequence, and by summarizing the findings of several articles, we further explained the mechanisms behind the three aspects that were not clearly explained enough in the two articles. Our results contradicted Singer and Ames' theory and supported that GC content distribution is largely random under UVR. We explained this by the G-T mutation counteraction and the evolutionary driving force caused by thymine dimer. We explained the cause of some exceptions, such as the function of genetic drift, photolyase and cryptochrome, and provided possible explanations for the low GC content in bacteria using neutral theory and selection theory.

We adopted an innovative method of shuffling the genomic sequence and comparing the double thymine content before and after shuffling to measure the tendency of the genomic sequence arrangement to favor the formation of thymine dimers. We also looked back and used new, integrated discoveries to help refine previously obscure and indefinite explanations, which is rare when most researchers focus on hot spots while some imperfections in the foundations may be overlooked.

However, there are also limitations to our studies. It should be noted that this study only examined the relationship between the formation of thymine dimers and UVR. How ROS damage can be correlated with UVR has unfortunately not been explored. Moreover, due to time constraints, we collected only one species of each genus we wanted to analyze – but did not use the mean of all species in each genus, which makes the study less rigorous. And we didn't include statistical analysis in our data because we didn't have enough data. With more time, the mean could be calculated and provide a more rigorous study. We can analyze more data to incorporate statistical analysis to ensure that our results are more meaningful. And the ancestors of bacteria can be reconstructed, so we can measure nucleotide change: the number of them that underwent the G to T mutation can be obtained, which can reflect the effect of ROS on the DNA sequence for us to measure the relationship between it and UVR.

We decide to further explore the relationship between ROS-induced damage and UVR in the future. We anticipate that more relationships between environmental factors and genomic sequences will be discovered. The study of UV damage may also provide more insights on possible treatments of the skin cancer.

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