14 The Ultraviolet Radiation Environment of Earth and Mars: Past and Present

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Exactly 130 years passed between the discovery by Isaac Newton that white light was composed of colors [1] and the discovery of ultraviolet radiation by Johann Wilhelm Ritter, a German electro chemist, in 1801. We now understand that ultraviolet radiation, although representing <2% of the total number of photons that reach the surface of present-day Earth, has had an important role in the evolution of life on Earth. This is because it has a high energy, energy being proportional to the frequency of the radiation. UV radiation is damaging to a number of key macromolecules, particularly DNA. On early Earth, the lack of an ozone column probably resulted in higher biologically weighted irradiance than the surface of present-day Earth as there were no other UV absorbers in the atmosphere. This is also the case for present-day Mars and probably was for Mars in its early history.

14.1 UV Radiation on Early Earth

Ultraviolet (UV) radiation has been a ubiquitous stressor since the origin of the first microbial ecosystems during the Archean era (3.9-2.5 Ga ago). Although the UV radiation that reaches the surface of the Earth spatially and temporally depends upon many factors [2], during the history of life on Earth four distinct periods of photobiology can be recognized [3]. Firstly, the period during which UV radiation influenced chemistry on prebiotic Earth during the Hadean era (>3.9 Ga ago). This includes the beneficial involvement of UV radiation in organic complexification as well as the deleterious effects it may have had on exposed prebiotic molecules. Since this does not involve ecosystems or organisms *per se*, it is not discussed here, although discussions can be found elsewhere [3-7]. The second stage involves the role of UV radiation during the Archean, when it is supposed that the Earth lacked a significant ozone column and was therefore exposed to higher fluxes of UV-B (280-320 nm) and UV-C (200-280 nm) radiation. The third stage is the transition phase. Atmospheric oxygen partial pressures and thus ozone column abundance rose and biologically effective irradiance on the surface of the Earth was reduced. The fourth phase is the period since this transition that covers the Proterozoic and Phanerozoic (2.5 Ga ago to the present), when life has been protected by the ozone column, but subject to alterations in the UV-B radiation regime as a result of short term changes in ozone column abundance caused by stochastic alterations in the astronomical environment, such as impact events and

supernovae [8] or endogenous events such as volcanism. It is the subject of this section to discuss what is known about the phase covering the Archean era (3.9-2.5 Ga ago).

14.1.1 UV Radiation During the Archean

The partial pressure of oxygen in the present-day atmosphere (~210 mb) is an imbalance caused principally by the activity of photosynthetic organisms, the burial of organic carbon and the lack of reductants from volcanic out-gassing and oceanic upwelling to mop up the oxygen so produced. A diversity of direct geologic and isotope evidence from Archean facies suggest that the Archean atmosphere was essentially anoxic. This is discussed elsewhere [e.g., 9, 10, 12-15]. The reasons for the lack of atmospheric oxygen in the Archean are still a point of discussion [e.g., 16-18]. Regardless of the mechanisms underlying the low atmospheric partial pressures of O_2 in the Archean and the arguments on the extent of oxygenic photosynthesis during this time, the photobiological consequences were identical - the early Earth lacked a significant ozone column and as a result it may have been subjected to much higher biologically effective irradiance than the present-day Earth.

In the absence of direct evidence, the effects of this photobiological environment can best be assessed using radiative transfer models that allow for the calculation of surface UV fluxes. Weighting functions can be used to calculate the biological effect of these fluxes. Because we are fairly sure that the basic structure of DNA has not changed since the Archean, action spectra for DNA damage [e.g., 19] can be useful for evaluating early Archean photobiology. Similar arguments also apply to photosystem II (PS II). The action spectra for isolated spinach chloroplasts [20] may seem an unlikely analogue for early PSs, but the experiments specifically examined the effects of UV radiation on PS II of the chloroplasts. Because PS II is similar in both chloroplasts and their non-symbiotic precursors, the cyanobacteria, this action spectrum is useful for gathering first order approximations of effects on cyanobacteria.

Once estimates of UV flux and weighted irradiance are made, then physiological responses of organisms to early environments can be assessed better.

14.1.1.1 Calculation of UV Radiation on Early Earth

The calculation of UV flux at the surface of the early Earth depends principally upon two factors - the luminosity of the early sun and the composition of the paleoatmosphere. At 3.5 Ga ago when there are unequivocal signs of life in the fossil record, the Sun was probably 25% less luminous than it is today [21, 22]. This might correspond to an approximately 25% lower flux across the UV range at wavelengths >270 nm based on the data presented by Zahnle and Walker [23] for solar fluxes at this time but with little change at lower UV-C wavelengths. These spectra are based on direct observations of young stars. The exact reductions in UV depend are model dependent [22], but ultimately, the assumptions that are made turn out to be of little consequence since the differences in weighted irradiances between early Earth and present-day Earth are overwhelmingly determined by the effect of the lack of ozone, not assumptions about whether the solar luminosity was between 0 or 35% lower. Nevertheless, our uncertainty about the UV output of the early Sun in the wavelength range of biological in-

terest is a limitation in our understanding. Early stars often emit more UV radiation at wavelengths below 200 nm [23-25]. These T-Tauri stars have been observed directly, and it is possible that during the formation of the Earth the Sun was emitting an intensity of UV radiation at these wavelengths 10 000 times greater than today and still four times greater at 3.5 Ga ago [24]. Because CO_2 absorbs wavelengths of UV radiation <200 nm, it is unlikely that T-Tauri emissions reached the surface of the Archean Earth.

The composition of the Archean atmosphere is not well known, but at 3.5 Ga ago, atmospheric composition may have been approximately 1 bar CO_2 [26] with N_2 partial pressures probably similar to today (~0.8 bar). An upper limit of 10 bar CO_2 has been suggested for the very early Archean [27], but this would lead to surface temperatures ~85 °C [26]. Investigations of pCO_2 ~2.7-2.2 Ga suggest values as low as 40 mb [28]. These latter values are consistent with the lower boundary for CO_2 suggested at this time in earlier work [26]. Thus, in general it is believed that pCO_2 was high in the early Archean decreasing into the Proterozoic.

These values can be used to derive the spectral irradiance of radiation reaching the surface of the Earth. The δ-2 stream method has been described previously and is a classical approach to calculating UV radiative transfer [29, 30]. In this approach, absorption is calculated according to Beers Law and the diffuse UV flux is calculated according to a series of equations that estimate the effects of scattering in the atmosphere. Both of these terms put together provide an approximation of the UV radiation at different wavelengths that actually reaches the ground from space. In Fig. 14.1 irradiances are shown for a zenith angle of 0° (sun overhead) for two atmospheric compositions (Early Archean at 3.5 Ga ago and late Archean at 2.7 Ga ago). Typical values for a zenith angle of 0° on present-day Earth are also shown. All cases assume cloudless skies. Clouds can have an effect on UV flux [2]. Integrated over time, comparisons between the photobiological environment of present-day Earth and early Earth could be influenced by cloudiness. But it is unlikely that the planet would have been 100% cloudy all of the time. Therefore, the calculations presented here still provide an upper boundary on instantaneous UV exposure.

The DNA weighted irradiances received at the surface of the Earth can be calculated for these atmospheres. In the high pCO_2 case (1 bar) the value is 54 W/m^2 using a DNA action spectrum normalized to 300 nm. For a pCO_2 of 40 mb, then DNA weighted irradiances would increase to ~101 W/m^2. These values can be convolved with present-day UV data to postulate an ultraviolet history for Earth as is shown in Fig. 14.2 [8].

Instantaneous exposure was much higher than today, but day length was shorter because of the effects of lunar tidal drag since that time. At 3-2.5 Ga ago day length may have been 14 hours [10]. The instantaneous DNA weighted irradiance would have been just over three orders of magnitude higher than today, but the daily weighted fluence would have been only 500 times greater. This would have had implications for the daily damage that a micro-organism would have had to repair and would have gone some way to off-setting the lack of an ozone column. However, it is clear that the overwhelming influence is the lack of an ozone column when comparisons are made to present-day Earth, not day length.

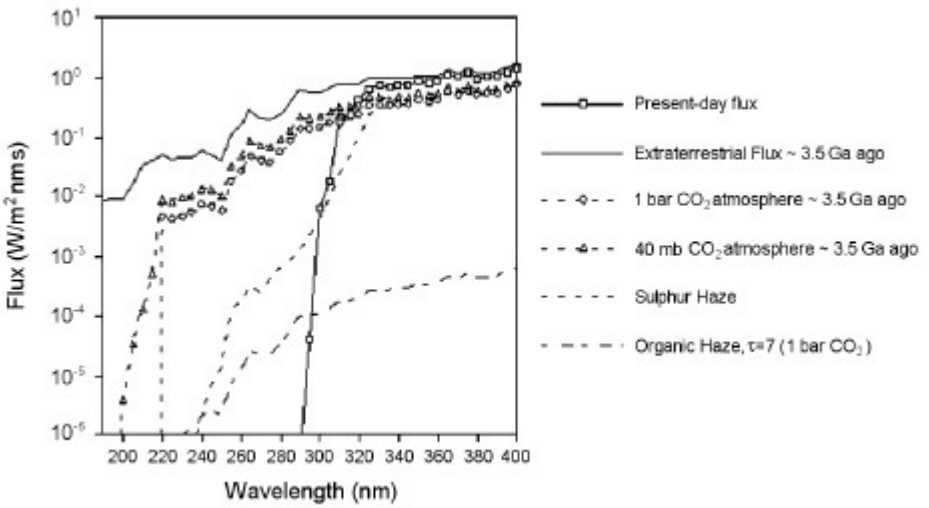

Fig. 14.1 Ultraviolet irradiance reaching the surface of Archean Earth for various assumptions about the composition of the atmosphere (see text for details).

14.1.1.2 Atmospheric Absorbers and Effects on Archean Photobiology

Trace quantities of other compounds could have profound consequences for UV exposure. Kasting et al. [31] investigated the surface UV effects of a sulfur haze in the early atmosphere caused by photolytic production of sulfur from SO_2 and H_2S volcanic outgassing. At high enough temperatures (~45 °C), sulfur could have reduced the integrated UV flux by up to seven times. The photochemical arguments for this scenario are uncertain. Figure 14.1 shows the photobiological consequences of a haze with a column abundance of ~1.5×10^{17} cm^{-2} as they envisaged.

A plausible contaminant in the early Earth atmosphere was a CH_4-generated hydrocarbon smog, the CH_4 produced either by early methogens or nonbiological processes [32]. This is analogous to early suggestions that an organic aldehyde haze may have provided screening on early Earth [4]. At an optical depth of 7 in the UV region, (optical depth being the natural logarithm of the ratio of radiation from a source over that seen by the observer – essentially a measure of attenuation), which has been suggested for early Earth [32], DNA-weighted irradiances would have been reduced to ~0.04 W/m^2, similar to exposed present-day Earth. Even modest smogs could have provided shielding for early life.

Finally, it has also been argued that appreciable levels of oxygen of 0.01-0.02 Present Atmospheric Levels (PAL) could have existed on early Earth. Numerous geological, physiological and biochemical arguments have been presented for this scenario [33, 34]. These oxygen levels which could result in ozone abundances ~4×10^{18} cm^{-2} would cause reductions in biologically effective irradiances by two orders of magnitude resulting in DNA weighted irradiances only two to three fold higher than typical

present-day values. Although not disproven, the geologic and isotopic evidence alluded to earlier is currently more consistent with an anoxic Archean atmosphere.

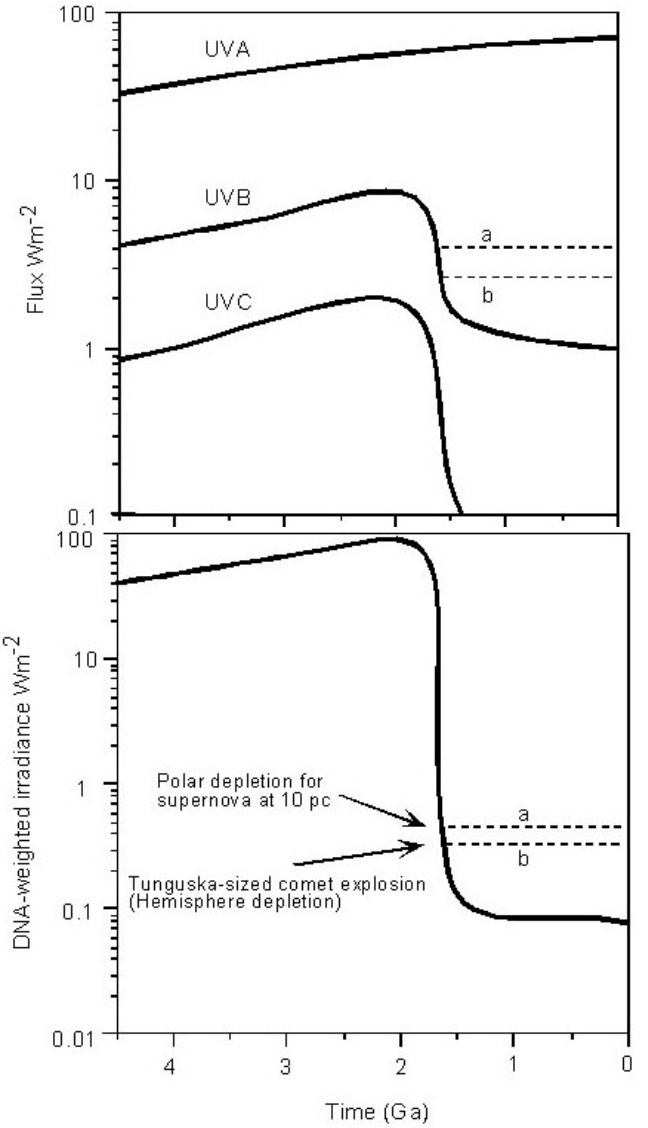

Fig. 14.2 The summarized photobiological history of Earth showing putative changes in UV-C, B and A at the surface of the Earth over time in the absence of UV absorbers in the atmosphere > 200 nm (see [8] for details). Also shown are corresponding changes in DNA-weighted biologically effective irradiances that might be expected from (a) a supernova explosion at 10 pc and (b) a Tunguska equivalent comet causing ozone depletion over a hemisphere.

14.1.2 Biological Effects of High UV Radiation Flux

The calculations shown here in an atmosphere lacking sulfur, CH_4 or ozone lead to DNA weighted irradiances two and a half to three orders of magnitude higher than on present-day Earth, similar to those presented previously [35-37]. Although a radiative transfer model was not used in [37] similar order of magnitude, differences were calculated. These differences in biologically effective irradiances have been confirmed in orbital experiments. Horneck and Rettberg [36, 38] used the extraterrestrial spectrum to observe inactivation of *Bacillus subtilis*. By measuring the change in Coomassie Blue staining, which is inversely proportional to the UV radiation received, they demonstrated that the biologically effective irradiances in Earth orbit were three orders of magnitude higher than on the surface of the Earth.

Assuming the worse case scenario (i.e. instantaneous DNA weighted irradiances were three orders of magnitude higher on Archean Earth than today), are there methods to cope with such an environment? What impact would it have on UV protection/repair and avoidance responses?

14.1.2.1 The Oceans

The oceanic water column could have been an effective screen for high UV flux. The water attenuation coefficients in the UV-C are almost an order of magnitude higher than those in the UV-B [39]. Expressed as a DNA-weighted irradiance at a depth of approximately 30 meters, irradiances could have been similar to the exposed surface of present-day Earth [8].

In the early Archean, the presence of upwelled ferrous iron could have provided additional UV attenuation. Holland suggests that ferrous iron concentrations could have been ~3 ppm [9]. With absorbance coefficients almost an order of magnitude higher than ferric iron, ferrous iron has been suggested as a potentially important UV screen [35, 40, 41]. However, if oxygenic photosynthesis existed in the early Archean, then ferrous iron could have been stripped from the photic zone. Certainly by the late Archean and early Proterozoic, when the prevalence of banded iron formations decreases [12, 13], it is likely that ferrous iron was exhausted as a screen. This could have happened before significant rises in atmospheric pO_2 [35].

Although much of the photic zone of many aquatic environments may have been clear during the early Archean and almost certainly by the late Archean, the photic zone could have been colonized by a low diversity, high UV resistant biota, which could have been numerically abundant [42]. A deep chlorophyll maximum that constitutes a deep region of high microbial abundance and quite high productivity could also have existed in the Archean as it does today [35, 42].

14.1.2.2 Intertidal and Terrestrial Habitats.

Examining a range of screening methods Cockell [37] concluded that there are a variety of substrates that provide over a two order of magnitude reduction of DNA-weighted irradiances and under such substrates, Archean organisms could be exposed to weighted irradiances similar to an exposed organism on present-day Earth. Admittedly, many fully exposed single-celled organisms on present-day Earth produce UV

screening compounds. Therefore, the comparison between biologically effective irradiances achieved by hiding under substrates and the exposed value on present-day Earth is not entirely accurate. However, it suffices in that we are considering order of magnitude reductions that many of these substrates provide compared to the full sky exposure.

Terrestrial habitats that would protect against UV radiation include the lithic habit (under or within rocks). In such substrates light levels are reduced to approximately 0.005% of incidence at depths, at which organisms [43] such as the cyanobacterium *Chroococcidiopsis*, are able to photosynthesize.

Reduced ferrous iron, which would have upwelled from the anoxic Archean oceans may also have protected some organisms in inter-tidal regions [35, 40]. As alluded to earlier, it could have been stripped from the water by an oxidized upper layer, but in inter-tidal regions it would have precipitated onto benthic habitats. Sediments can also provide UV protection. Garcia-Pichel and Bebout found that UV-B was reduced to 1% between 1.25 and 0.23 mm from the surface [45].

Protection of organisms may be enhanced by the matting habit, whereby the upper layer of dead organisms protect organisms underneath by virtue of their UV screening compounds. Margulis et al. [16] showed that after 3 days of continuous exposure to 254 nm radiation, a protected *Lyngbya* sp. community was still viable, although cells on the surface were killed after minutes. This matting habit is well preserved in the Archean fossil record in the form of stromatolitic layering in microbial communities [46]. Indeed, it is probably the only UV protection strategy that we can truly support with confidence based on real fossil record evidence.

14.1.2.3 Ultraviolet Radiation Screening Compounds and Repair

The evolution of UV screening compounds such as mycosporine-like amino acids (MAAs) which can screen in the UV-B and A [46, 47] as well as scytonemin, a UV-A screening compound associated with terrestrial cyanobacteria [48] would have led to important versatilities in the colonization of exposed habitats [35]. Garcia-Pichel reviews the role of these compounds in the evolution of cyanobacteria [35]. Organisms may also have been exposed to fluxes of UV-C radiation. The cyanobacterial sheath compound scytonemin has an absorbance peak at 250 nm. Experimental results showed that scytonemin can absorb UV-C radiation to an extent that is physiologically advantageous to photosynthetic carbon fixation in *Tolypothrix* sp. isolated from exposed rock surfaces [49] as well as *Calothrix* and *Chroococcidiopsis* sp. [50]. Most organics possess UV-C absorbance and are likely to have a physiologically beneficial effect against UV-C [37]. For example, plant flavonoids can provide significant protection against UV-C-induced photosynthesis inhibition in pea (*Pisum sativum* L.) [51], which certainly did not exist in the Archean! Like scytonemin, flavonoids have an absorbance peak at ~250 nm. It is likely that a diversity of organics in the upper layers of microbial mats would absorb UV-C radiation, particularly if upper layers contain a dead layer of microorganisms, from which organics would be released and subsequently photolytically degraded into smaller UV absorbing organics.

Thus, data on UV screening compounds demonstrates that biological protection against the complete UV range from 200-400 nm was probably achieved on early Earth and that despite the high energy and biological destructiveness associated with UV-C

radiation, the fact that it is absorbed by most organics it passed through, probably made it one of the less challenging regions of the UV spectrum to deal with. Higher wavelengths required more specific evolutionary innovations.

Protection, either physical or biological, is never 100% efficient and the repair of DNA must also have been a key response to UV radiation that penetrated the cell.

The evidence of repair processes in the deep-branching Archaea that includes photoreactivation [52], recombination repair [53] and excision repair [52] suggest that the major pathways of repair seen in present-day organisms were developed in the Archean. Indeed, photolyase, a 310-500 nm inducible enzyme responsible for photoreactivation has been suggested to be an early photoreceptor [54]. Some of these repair processes are quite impressive. For example, the archeon-*Thermococcus stetteri* is two to three more times sensitive to gamma irradiation than *Deinococcus radiodurans* [55], but this is still a significant repair capability. *D. radiodurans* itself comes close to being able to tolerate the worse case UV environment of early Earth based on theoretical calculations. It demonstrates that repair alone might have been sufficient to deal with a high Archean UV flux [42].

In studies directed at Archean conditions, Pierson et al. demonstrated a UV tolerance in *Chloroflexus aurantiacus*, an anoxygenic photoheterotroph from the deepest branches of the eubacterial line [56]. Photoreactivation of damage caused by 254 nm UV-C radiation was also shown in the obligate anaerobe *Clostridium sporogenes*, which was suggested to be a legacy of pre-Phanerozoic evolution [57].

A further complication in developing a detailed knowledge of responses to a putatively higher Archean UV radiation regime is that the trade-off between protection and repair is quite varied. It depends upon the different energetic demands in different organisms and probably habitat. In a recent study it was found that photosynthesis in two organisms, the cyanobacterium *Lyngbya aestuarii* and a green alga *Zygogonium* sp. was affected by ambient UV-B and UV-A radiation even though these organisms do possess UV-B screening compounds and in the case of *Lyngbya*, UV-A screening scytonemin [58]. However, in the red alga *Cyanidium caldarium* which does not possess UV screening compounds, photosynthesis inhibition by UV radiation was negligible. This may be caused by different nutritional status but could also be caused by higher rates of repair.

14.1.2.4 Photosynthesis in the Archean

The effects of Archean UV flux on other physiological responses can be estimated. The action spectrum for PS II inhibition shows a markedly greater involvement of the UV-A region than the action spectrum for thymine dimer formation in DNA [20]. Although UV radiation can affect other parts of the photosynthetic apparatus (e.g., the photosynthetic enzyme D-ribulose 1,5-bisphosphate carboxylase-oxygenase, RuBisCO), the PS II action spectra is broadly similar to the action spectra for photosynthesis inhibition in whole organisms and so is a useful proxy for UV-induced photosynthesis inhibition in cyanobacteria and similar organisms. The UV-A contribution corresponds to the role of reactive oxygen species in PS damage. Because UV-A levels are actually higher today than in the Archean because of the more luminous Sun, this part of the spectrum would have made a lesser contribution on Archean Earth, offsetting some of

the effects of greater UV-B and UV-C flux. This is why some workers have calculated that PS damage was less great in the Archean compared to DNA damage [35, 37].

14.1.3 Beneficial Effects of High UV Radiation on Archean Earth?

Insofar as UV radiation is a mutagen, then it might be expected that a two to three order of magnitude higher DNA-weighted irradiance on early Earth could lead to higher mutation rates. Then one could postulate that this might ultimately lead to higher microbial biodiversity or a greater number of mutations would have allowed faster adaptation to changing environmental conditions compared to today.

The idea is intriguing, but qualitative evidence from the Archean fossil record does not lend strong support. The microbial biodiversity of the Archean is not greater than the Proterozoic, although this may be largely a function of lack of preservation of the Archean fossil record [59]. Furthermore, cyanobacterial hyperbradytely (the extreme lack of evolutionary change in a group of organisms) is embodied in the morphological characteristics and habitat preferences of cyanobacterial stromatolites and microfossils, both modern day and their postulated Archean counterparts [59]. This evidence suggests that in fact many of the members of this phylum have not changed much, rather than being subject to great evolutionary change during the Archean as a result of UV-induced mutations. Indeed, evolutionary radiation and specialization seems to be a characteristic more of the Phanerozoic era rather than the Precambrian.

Morphometric data does not necessarily imply similar physiologies. It is plausible that higher rates of mutation may simply increase the rate of change of physiology. However, evolutionary changes and mutations normally, over time, engender morphological changes as habitat and physiology change in response to new environmental opportunities and challenges. The conservative nature of the distribution of morphologies of Archean micro-fossils in comparison to modern day cyanobacteria, particularly the Oscillatoriaceae and Chroococcaceae, as well as their similar habitats (such as inter-tidal stromatolites) might suggest physiological hypobradytely as well. Indeed, cyanobacteria are generalists [59].

UV radiation has been suggested to have other positive roles in the Archean biosphere. It has been postulated to be a trigger for the evolution of sex [16, 60]. The concept is an extension of sex as an error repair mechanism [e.g., 61]. Recombination repair, whereby new genetic material may be used to repair UV damaged DNA bears functional similarities to meiotic recombination and insofar as UV radiation causes mutations, sex has been suggested to have been stimulated by the need to repair UV-induced DNA damage [60]. Elena and Lenski [62] provide some evidence that mutations are likely to be antagonistic as much as they are synergistic and so they suggest that sex is not a good way to reduce mutational load. Nevertheless, it is clear that a population will inexorably collect mutations over time through unfaithful replication of information, the so-called "Muller's ratchet" [63] and mechanisms that allow for improved methods of transferring new information in a population might be expected to reduce mutational load [60].

14.2 The Ultraviolet History of Mars and Venus: An Exercise in Comparative Evolutionary Photobiology

The atmosphere of Mars is 95.3% CO_2 and so the radiative transfer calculations that we use to calculate the surface UV environment can essentially assume a pure CO_2 atmosphere (see [64]). Unlike the Earth, Mars does not have a significant ozone column, although some ozone build-up occurs over the poles in spring and winter. These levels, although about two orders of magnitude lower than typical terrestrial column abundances, can reduce UV-C flux reaching the ground [64, 65]. The photobiological history of the planet has been almost exclusively determined by the increase in solar luminosity over time and change in the atmospheric carbon dioxide reservoir. Haberle et al. carried out a detailed modeling study of the evolution of CO_2 on Mars over time [66]. They investigated varying initial CO_2 inventories as well as alterations in solar luminosity and the greenhouse effect. They ultimately conclude that none of the outcomes is entirely satisfactory. Large initial CO_2 inventories tend to predict Martian polar caps that are too large compared to the ones we observe today. Smaller inventories require low partial pressures of CO_2 on early Mars, which may be inconsistent with a warmer, more water rich past [67].

In view of the warmer conditions proposed for early Mars, Haberle et al. [66] propose a scenario where the initial CO_2 inventory may have been between 0.5 and 3 bar. At approximately 3.8 Ga, the CO_2 inventory may have been 0.5-1 bar. How the CO_2 atmospheric reservoir then evolved to current conditions (the present-day surface pressure is on average ~6 mb) is unknown. Either the CO_2 was slowly lost to carbonates, or the atmosphere may have collapsed. In the latter scenario the build-up of the polar ice caps results in reduced temperatures and a freeze out of CO_2. A feedback process is initiated, which leads to a collapse of the atmospheric CO_2 reservoir [66]. Because of the direct coupling between the Martian polar caps and atmospheric CO_2, the time to reach equilibrium may have been only ~200 years [68]. In Fig. 14.3, the photobiological history of Mars has been presented for an initial inventory of 2 bar declining to 1 bar in the time corresponding to the early Archean (the Martian Noachian) with an arbitrary gradual decline to present-day conditions. The rate of decline of CO_2 varies with the models used [66, 69].

The rising UV flux over time, although theoretically presenting an increasing photobiological challenge, probably does not prevent the evolution of life. The present-day DNA-weighted irradiance on the surface of Mars is similar to the weighted irradiance on the surface of Archean Earth, the biological significance of which has been discussed [37]. The photobiological deterioration of Mars could theoretically exacerbate the demise of life in synergy with other physical factors [37]. Low temperature extremes and the possible existence of peroxides in the Martian soil are two environmental stressors detrimental to life, but the lack of liquid water over most of the present-day surface is undoubtedly the worst [69].

This gradualist view of the ultraviolet history of Mars may have been different if the planet did suffer an atmospheric collapse during its history between 4.5 and 3 Ga ago [66]. A planetary atmospheric collapse has the potential to trigger an ultraviolet crisis. A reduction of the Martian atmospheric CO_2 reservoir from ~1 bar to ~6 millibar would increase DNA-weighted biologically effective irradiances by five-fold. A reduction from 0.5 bar to ~6 millibar would cause a three-fold increase.

Finally, Mars may have experienced periods of *reduced* UV radiation even since 3.5 Ga ago. Gulick et al. [70] suggest that episodic CO_2 releases of up to 2 bar resulting from catastrophic floods may have occurred. Such episodes would have resulted in an ultraviolet amelioration as illustrated in Fig. 14.1. The possibility of UV

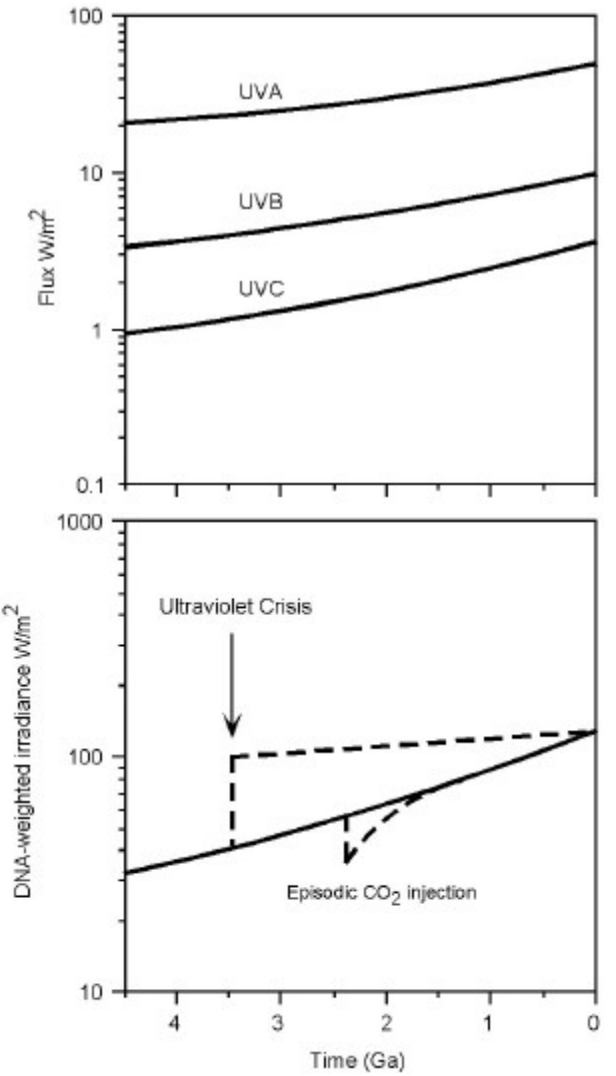

Fig. 14.3 The ultraviolet history of Mars. The graph of biologically effective irradiances also shows the theoretical photobiological consequences of an 'ultraviolet crisis' caused by an atmospheric collapse. Also shown are the effects of episodic CO_2 injections.

amelioration events should be noted, since regardless of whether there was life on

Mars or not, they represent periods of increased biological potential.

Venus has a very different ultraviolet history [8]. On Venus, we suppose that the early atmosphere was thinner that it is today. As solar luminosity increased so the early water inventory was eventually lost into a runaway greenhouse effect. The water would have been photolyzed, the hydrogen disappearing into space and the oxygen lost in oxidation reactions with surface rocks. As weathering ceased in the absence of water, so there was no way for the CO_2 in the atmosphere to return to the crust, the result was the dense 9.5 MPa atmosphere we observe today. The atmosphere is in fact so dense that no UV-C or UV-B radiation reaches the surface of the planet and only very small amounts of UV-A penetrate. Thus, in a relatively short space of geological time, Venus probably went from a planet exposed to quite harsh UV radiation to one, on which the surface UV regimen is now absolutely clement. This is interesting, because the surface of Venus today is lifeless; the high (464 °C) temperature exceeds the known upper bounds for biology. Thus, Venus demonstrates nicely the unimportance of UV radiation as an evolutionary selection pressure when other factors, particularly lack of water, become limiting to life.

14.3 Conclusions

Over the past two centuries, since the discovery of UV radiation, information on the responses of micro-organisms to this agent has allowed us to develop an understanding of the role of UV radiation as an environmental stressor over geologic time periods. This perspective on Earth history is really only complete when this piece of the jigsaw is placed against others. Thus, efforts to understand the history of UV radiation on Mars can allow us to pursue an investigation of comparative evolutionary photobiology [8], elements of which were presented here. Examination of the history of UV radiation on Venus, for instance [8, 71] can extend our understanding yet further. With these perspectives in mind, we can understand better the importance, or lack of importance, of UV radiation in influencing biological evolution on planetary surfaces.

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