

Ecosystems, Evolution, and Ultraviolet Radiation

Charles S. Cockell Andrew R. Blaustein
Editors

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Preface

In 1928, Harry Marshall speculated on the role of ultraviolet radiation in extinction (Marshall, H.T. 1928. Ultra-violet and extinction. *American Naturalist* 62:165–187). He speculated that volcanoes could throw dust into the atmosphere, blocking out ultraviolet light and causing rickets in animals, which would then perish. Perhaps a search for an increase in the incidence of rickets manifested in fossil bones would reveal past episodes of alterations in the ultraviolet environment. At the time his hypothesis was undoubtedly regarded as bizarre. The paper is rarely to be found referenced in any subsequent discussion on the role of physical factors in shaping evolution or in any discourse on catastrophism.

The reasons for the disappearance of this quite prescient work into history are probably twofold. First, at the time little was known about the biological effects and importance of ultraviolet radiation as a stressor and selection pressure. Models of atmospheric factors that might influence the surface UV regime were crude. There was no way to quantitatively constrain the ideas presented and so, it was probably thought, the idea had little merit beyond speculation. Second, the lack of knowledge on the biological effects of UV radiation meant that the next step—considering the evolutionary consequences of altered UV radiation regimes—could hardly be embarked upon with any confidence.

In this volume, we return to the idea of UV radiation, its effects on ecosystems, and the likely evolutionary consequences of changed UV radiation environments, past, present, and future. The first two chapters examine the history of the UV radiation climate of earth and the factors that determine organismal and ecosystem exposure. Their purpose is to give the reader a physical perspective on UV radiation and an understanding of the constantly changing UV environment to which ecosystems are exposed. Variations in the UV radiation environment occur at the local level (such as boundary layer and plant canopy effects) through to global-scale changes (such as alterations in the column abundance of UV-B-protecting ozone). UV radiation regimes also vary over temporal scales. These alterations occur on time scales of seconds (the movement of clouds and plant canopies) to literally billions of years (gross long-term changes in the composition of the Earth's atmosphere).

In the chapters that follow, five specific biological and ecological topics in photobiology are considered—the effects of UV radiation on amphibians, plants,

corals, aquatic microbial ecosystems, and, finally, Antarctic ecosystems that are exposed to the anthropogenically generated ozone "hole." These chapters consider UV radiation effects at a diversity of levels from the biochemical to the community. Their purpose is to provide the reader with our current understanding of the ecological effects of UV radiation, and the areas in which questions still remain, and to provide a perspective from which the reader can better understand questions in evolutionary photobiology. The final chapter investigates the biological consequences of extraterrestrial ultraviolet fluxes, which are quite different from those experienced on the Earth.

Our knowledge of the role of UV radiation in shaping ecology and evolutionary change is still in its infancy. In this volume, we bring together a number of authors with the aim of helping to consolidate a better understanding of this interesting area of photobiology.

Cambridge, UK
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1

A Photobiological History of Earth

CHARLES S. COCKELL

Ultraviolet radiation has been a ubiquitous physical stressor since the origin of the first microbial ecosystems during the Archean era (3.9–2.5 Ga [billion years] ago). Although the UV radiation that reaches the surface of the Earth spatially and temporally depends on many factors (Xenopoulos and Schindler, Chapter 2, this volume), during the history of life on Earth four distinct periods of photobiological history can be recognized (Cockell and Knowland 1999). First, the period during which UV radiation influenced chemistry on prebiotic Earth during the Hadean era (>3.9 Ga ago) dominated by the involvement of UV radiation in organic complexification as well as the deleterious effects it may have had on exposed prebiotic molecules. Because this does not involve ecosystems or biological organisms per se, it is not discussed in detail here, although discussions on the role of UV radiation on prebiotic Earth can be found elsewhere (Sagan 1973; Kolb, Dworkin and Miller 1994; Cleaves and Miller 1998; Bernstein et al. 1999; Cockell and Knowland 1999).

The second stage involves the role of UV radiation during the Archean era when it is supposed that the Earth lacked a significant O₃ (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 O₂ (oxygen) partial pressures and thus O₃ column abundances rose, and biologically effective irradiances on the surface of the Earth were reduced. The fourth phase is the period since this transition that covers the Proterozoic and Phanerozoic (2.5 Ga ago to the present). During this period, life has been protected by the O₃ column but subjected to alterations in the UV-B radiation regime as a result of short-term changes in O₃ column abundances caused by either natural variations or stochastic alterations in the astronomical environment.

This chapter discusses what is known about each of these phases.

UV Radiation from the Archean to the Archean–Proterozoic Transition

The partial pressure of O₂ in the present-day atmosphere (~210 millibars [mb]) is an imbalance caused principally by the activity of photosynthetic organisms, the burial of organic carbon, and the lack of reductants from volcanic outgassing

and oceanic upwelling to mop up the O₂ so produced. A diversity of direct geologic and isotopic evidence from Archean facies suggests that the Archean atmosphere was essentially anoxic. These data include the lack of red beds before 2.0 Ga ago, the deposition of easily oxidizable uraninites in rocks older than 2.3 Ga, and the concentrations of rare-earth metal ions in Archean sedimentary rocks that are not enriched, unlike their Phanerozoic counterparts. The increased formation of sulfate deposits at about 2.5 Ga ago and an increase in the niobium/thorium ratio from about 3 Ga to 2 Ga ago, as well as the disappearance of banded iron formations formed from reduced iron, further support this picture (e.g., Holland 1984; Walker et al. 1983; Holland and Beukes 1990; Holland 1994; Lowe 1994; Walker and Brimblecombe 1985; Collerson and Kamber 1999).

The reasons for the lack of atmosphere O₂ in the Archean are still a point of discussion. Either a greater flux of reductants, particularly hydrogen, mopped up O₂ being produced by oxygenic photosynthesizers in the earliest period of the Archean (Margulis, Walker and Rambler 1976; Schopf, Hayes and Walter 1983) or oxygenic photosynthesis was a later innovation and thus there was limited O₂ production in the Archean. Alternatively, oxygenic photosynthesizers did exist in the Archean, but primary productivity was low (Knoll 1979), which plausibly could be caused by a lower biomass of autotrophs during a period when anaerobic chemoheterotrophs may have dominated the Earth's microbial ecosystems (Schopf, Hayes and Walter 1983).

Numerous arguments suggesting the presence of oxygenic photosynthesis in the Archean have been previously presented (Schopf 1994, and discussions therein). Microbial communities inhabited the Earth as early as 3.5–3.3 Ga ago (Schopf and Packer 1987) and probably as early as 3.8 Ga ago (Mojzsis et al. 1996). Many of these microfossils, which possess coccoid and filamentous forms, bear strong morphological similarities with extant cyanobacteria, suggesting that this phylum may have existed as early as 3.5 Ga ago (Schopf 1994). Of course, morphological similarities do not necessarily imply physiological similarities (Schopf 1994). Nevertheless, these Archean organisms apparently existed as intertidal stromatolites. The habitat similarities of these organisms, as well as their morphological similarities to present-day cyanobacteria, thus suggest that they may have been oxygenic photosynthesizers (Schopf 1994).

Regardless of the mechanisms underlying the low atmospheric partial pressure of O₂ 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 O₃ column and as a result it might have been subjected to much higher biologically effective irradiances than the present-day Earth. Results using a photochemical model and assumptions about the temperature of early Earth suggest that, at 3.5 Ga ago, O₂ levels were at most $\sim 1 \times 10^{-4}$ PAL (present atmospheric level) and possibly much lower (Kasting 1987). At these partial pressures, the O₃ column abundance would have been insufficient to reduce biologically effective irradiances by any significant fraction.

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. As we are fairly sure that the basic structure of DNA has not changed since the Archean, action spectra for DNA damage (Green and Miller 1975) can be useful for evaluating early Archean photobiology. Similar arguments also apply to photosystem II. The action spectra for isolated spinach chloroplasts (Jones and Kok 1966) may seem an unlikely analogue for early photosystems, but the experiments specifically examined the effects of UV radiation on photosystem II. Because PSII is similar in chloroplasts and their nonsymbiotic precursors, the cyanobacteria, this action spectrum is useful for gathering first-order approximations.

Once these estimates of UV flux and weighted irradiance are made, then physiological responses of organisms to early environments can be assessed. There are two approaches to examine the consequences of these calculated fluxes on early microbial ecosystems. First, modern analogue organisms such as cyanobacteria can be used. Because of the diversity of gross morphological similarities between present-day and Archean–early Proterozoic fossils, (such as the stromatolitic matting habitat in which organisms lower in the stratified community can get the advantage of UV protection from organisms in the upper layers), these models for coping with UV radiation can be used to understand possible responses of Archean communities (Pierson, Mitchell and Ruff-Roberts 1993). The approach reaches a useful limit: This limit is when specific physiological responses are considered based on modern organisms, such as, for example, the efficacy of DNA repair processes. Over the past 3.5 billion years, Archean microorganisms have evolved into mammoths, moths, and astronauts, and so although morphological and habitat characteristics of Archean cyanobacteria may well be similar to present-day organisms, as alluded to earlier, there is considerable latitude for changes in internal physiological responses and biosynthetic pathways.

With these uncertainties a second approach is useful—to find the upper limits of UV tolerances on present-day Earth and to compare these to the radiation environments suggested for early Earth. If present-day organisms can be demonstrated to possess adequate physiological responses to those theoretically required on early Earth, then it is probably an acceptable interpolation to suggest that such survivorship may have existed on early Earth.

Calculation of UV Radiation on Early Earth

The calculation of UV flux at the surface of the early Earth depends on two principal components: 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 (Newman and Rood 1977; Gough 1981). This difference might correspond to an approximately 35% lower flux across the UV range of biological interest, based on the

data presented by Zahnle and Walker (1982) for solar fluxes at this time. These spectra are based on direct observations of young stars. The exact reductions in UV depend on the degree to which the reduction of solar luminosity was a function of lower temperature (thus changing the spectral distribution of the radiation) or a smaller radius of the sun (just changing total output) (Gough 1981). These discussions have been presented elsewhere, but ultimately the assumptions that are made turn out to be of little consequence, because the differences in DNA-weighted irradiances between early Earth and present-day Earth are overwhelmingly determined by the effect of the lack of O₃, not assumptions about whether the solar luminosity was between 25% and 35% lower.

Early stars often emit considerably more UV radiation at wavelengths below 200 nm (Zahnle and Walker 1982; Canuto et al. 1982, 1983). These T-Tauri stars have been observed directly, and it is possible that during the formation of the Earth our own sun was emitting an intensity of UV radiation at these wavelengths 10,000 times greater than today and still 4 times greater 3.5 Ga ago (Canuto et al. 1982). Because CO₂ (carbon dioxide) absorbs wavelengths of UV radiation below 200 nm, it is unlikely that T-Tauri emissions reached the surface of the Earth. They may have had significant effects on the chemistry of the paleoatmosphere, although calculations suggest that O₃ production by these emissions would not be sufficient to significantly alter surface UV flux, with O₃ column abundances being generally less than $1 \times 10^{16} \text{ cm}^{-2}$ (Canuto et al. 1982, 1983).

The composition of the Archean atmosphere is not well known, but at 3.5 Ga ago, atmospheric composition may have been approximately 1 bar CO₂ (Kasting 1987), with N₂ (nitrogen) partial pressures probably similar to those today (~0.8 bar). An upper limit of 10 bar CO₂ has been suggested for the very early Archean (Walker 1986), but this would lead to surface temperatures of about 85°C (Kasting 1987). Investigations of pCO₂ at the Archean-Proterozoic transition at about 2.7–2.2 Ga suggest values as low as 40 mb (Rye, Kuo and Holland 1995). These latter values are consistent with the lower boundary for CO₂ suggested at this time in earlier work (Kasting 1987).

These values can be used to derive the spectral irradiance of UV radiation reaching the surface of the Earth. The direct UV flux reaching the ground is calculated according to Beer's law, and the diffuse UV flux is calculated according to a Delta-Eddington approximation. This δ -2 stream method has been described previously and is a classical approach to calculating UV radiative transfer (Joseph, Wiscombe and Weinman 1976; Haberle et al. 1993). In Figure 1.1, 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 shown. All cases assume clear cloudless skies. Clouds can have an effect on UV flux (Xenopoulos and Schindler, Chapter 2, this volume). Integrated over time, comparisons between the photobiological environment of present-day Earth and early Earth could be strongly influenced by cloudiness. It is unlikely, however, that the planet would have been 100% cloudy all the time; therefore, the calculations presented here still provide an upper boundary on instantaneous UV exposure.

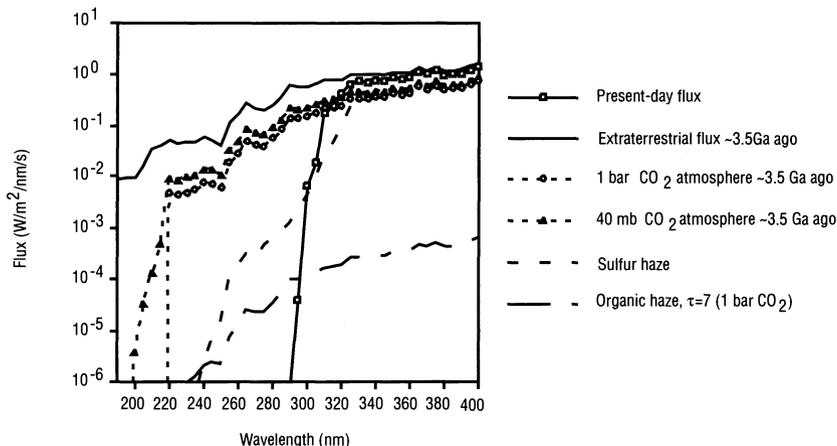


FIGURE 1.1. UV irradiance reaching the surface of the Archean Earth for various atmospheric scenarios described in the text. Data are for a zenith angle of 0° . Two CO_2 partial pressures are provided for 3.5 Ga.

The DNA-weighted irradiances received at the surface of the Earth may 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, DNA-weighted irradiances increase to approximately 101 W/m^2 . Table 1.1 shows some selected effective irradiances for various early Earth scenarios, and Figure 1.2 shows the action spectra used to calculate these values.

Archean Day Length

Instantaneous exposure was much higher than today, but day length was shorter. At 3–2.5 Ga ago, day length may have been 14 h (Walker et al. 1983); this is because the Earth has undergone a tidally induced slowing of its rotation rate caused by the presence of a moon. If we assume that obliquity was about the same—and it has been suggested that the Earth’s obliquity is moon stabilized

TABLE 1.1. Weighted irradiances for various atmospheric scenarios discussed in the text.

Atmosphere	DNA-weighted irradiance	Photosystem inhibition
Present-day value	0.071	17.5
1 bar CO_2 , 0.8 bar N_2 (~3.5 Ga ago)	54.1	16.3
40 mb CO_2 , 0.8 bar N_2 (~3–2.7 Ga ago)	101	26.3
40 mb CO_2 atmosphere with sulfur haze at $1.5 \times 10^{17} \text{ cm}^{-2}$	3.41	9.54
Organic haze in atmosphere, $\tau = 7$	0.034	0.013

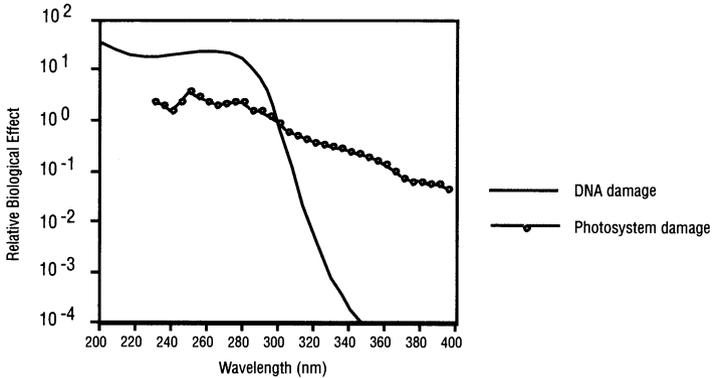


FIGURE 1.2. Action spectra for DNA damage and photosystem inhibition described in the text and used to calculate the Archean biologically effective irradiances described in this chapter.

(Laskar, Joutel and Robutel 1993)—then although the instantaneous DNA-weighted irradiance would have been just over three orders of magnitude higher than today, the daily weighted fluence would have been only 500 times greater because of shorter day length (Cockell 1999a) at any comparable latitude. This difference would have had implications for the daily damage that a microorganism would have had to repair and would have gone some way to offsetting the lack of an O_3 column. However, it is clear that the overwhelming influence is the lack of an O_3 column, not day length, when comparisons are made to present-day Earth (see Table 1.1).

The values calculated here are for a worse case scenario. They assume cloudless skies without any UV absorbers in the Archean atmosphere other than CO_2 . Could other factors have altered surface UV flux?

Atmospheric Absorbers and Effects on Archean Photobiology

Although we can make quite robust investigations of the effects of changing CO_2 and N_2 partial pressures on the UV climate of early Earth, trace quantities of other compounds could well have had profound consequences for UV exposure. Kasting et al. (1989) investigated the surface UV effects of a sulfur haze in the early atmosphere caused by photolytic production of sulfur from SO_2 (sulfur dioxide) and H_2S (hydrogen sulfide) volcanic outgassing. At high enough temperatures ($\sim 45^\circ C$), sulfur could have reduced the integrated UV flux by as much as sevenfold. The photochemical arguments for this scenario are uncertain. It would have required a CO_2 partial pressure exceeding 2 bar, which is contentious. Figure 1.1 and Table 1.1 show the photobiological consequences of a haze with a column abundance of $\sim 1.5 \times 10^{17} \text{ cm}^{-2}$ as they envisaged.

A plausible contaminant in the early Earth atmosphere was a CH₄-generated hydrocarbon smog, the CH₄ (methane) produced by either early methanogens or nonbiological processes (Sagan and Chyba 1997). This idea is analogous to early suggestions that an organic aldehyde haze may have provided screening on early Earth (Sagan 1973). Organic molecules are effective UV absorbers. At an optical depth of 7 in the UV region, which has been suggested for early Earth (Sagan and Chyba 1997), DNA-weighted irradiances would have been reduced to approximately 0.04 W/m², similar to exposed present-day Earth (see Figure 1.1 and Table 1.1). Even modest smogs could have provided shielding for early life.

Finally, it has also been argued that appreciable levels of O₂ (0.01–0.02 PAL) could have existed on early Earth. Numerous geologic, physiological, and biochemical arguments have been presented for this scenario (Towe 1996). These O₂ levels, which could result in O₃ abundances $\sim 4 \times 10^{18}$ cm⁻², would cause reductions in biologically effective irradiances by two orders of magnitude, resulting in DNA-weighted irradiances only two- to threefold 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.

Biological Effects of High UV Radiation Flux

Let us assume that such atmospheric absorbers did not exist and that UV exposures were the maximum that radiative transfer calculations suggest. What would be the effect of these irradiances, and would they really be influential in the biogeographic distribution of life, either on land or in the photic zone of aquatic environments?

The calculations shown here 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 (Garcia-Pichel 1998; Rettberg et al. 1998; Cockell 1998). Although a radiative transfer model was not used by Cockell (1998), similar order of magnitude differences between early and present-day Earth were calculated. These differences in biologically effective irradiances have been directly confirmed in orbital experiments. Rettberg et al. (1998) used the extraterrestrial spectrum in Earth orbit to calculate loss of viability 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. Garcia-Pichel demonstrated DNA-weighted irradiances on early Earth two orders of magnitude higher using an action spectrum for killing *Escherichia coli* under anoxia (Garcia-Pichel 1998). The slightly lower value calculated could be because UV fluxes were calculated from the expected reductions in blackbody flux from the sun, assuming that the reduction in solar luminosity was caused by a temperature change. These values give slightly lower UV fluxes than the assumption of 35% reduction in luminosity taken in this chap-

ter. However, the qualitative conclusions in all these works are essentially identical. They demonstrate that the Archean environment was one in which DNA damage to exposed phototrophs could have been very substantially higher than today.

Methods for Coping with UV Flux on Early Earth

Even under the highest UV radiation fluxes that are calculated, many mechanisms could have existed on a microbially dominated Archean Earth to screen UV radiation effectively. A number of these have been discussed previously, and some are reviewed here with some new data.

The Oceans

The oceanic water column would have been an effective screen. UV-B radiation can penetrate to significant depths into the present-day oceans, with 1% of incident radiation recorded at a depth of 50 meters (m) in some Antarctic waters (Smith et al. 1992). The penetration of short UV wavelengths into water led originally to suggestions that impurities such as iron and nitrogenous salts might have been important for life in the photic zone (Margulis et al. 1976). Although these substances might have provided additional protection (see following), the water attenuation coefficients in the UV-C are almost an order of magnitude higher than those in the UV-B (Smith and Baker 1981). Biologically damaging UV-C is quite quickly attenuated. Figure 1.3 shows the attenuation of wavelengths between 200 and 750 nm in the late Archean oceans and present-day oceans (Cockell 2000b). Expressed as a DNA-weighted irradiance (Figure 1.4) at a depth of approximately 30 m, irradiances could have been similar to the exposed surface of present-day Earth.

In the early Archean, the presence of upwelled ferrous iron could have provided additional UV attenuation in the oceans. Holland suggested that ferrous iron concentrations could have been about 3 ppm (Holland 1984). With absorbance coefficients almost an order of magnitude higher than ferric iron, ferrous iron has been suggested as a potentially important UV screen (Olson and Pierson 1986; Pierson, Mitchell and Ruff-Roberts 1993; Garcia-Pichel 1998). However, if oxygenic photosynthesis had existed in the early Archean then this 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 (Lowe 1994; Holland 1994), it is likely that ferrous iron was exhausted as a screen and that this could have happened before significant rises in atmosphere pO_2 occurred (Garcia-Pichel 1998).

Other UV absorbers encountered in the present-day oceans were probably not available. The lack of colonization of land by plants, together with the putatively smaller area of exposed continental cratons (Veizer 1983), would have meant fewer humic substances and less allochthonous carbon in the oceanic photic zone,

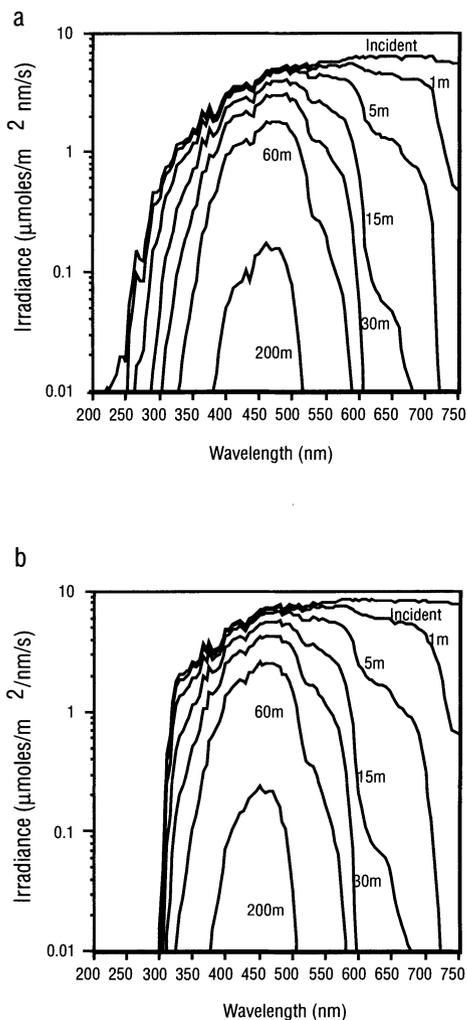


FIGURE 1.3a,b. Spectral irradiance penetrating into (a) the Archean oceans assuming a 40 mb CO_2 , 0.8 bar N_2 atmosphere and (b) present-day oceans for a zenith angle of 0° .

making the waters quite clear except in localized areas of high productivity where dissolved organic carbon could have come from autochthonous sources, such as in coastal regions.

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, as Figure 1.4 suggests, the photic zone could have been colonized by a low-diversity, high-UV-resistant biota that could have been numerically abundant (Cockell 2000a,b). The photic zone of many Archean water bodies could well have been oligotrophic. However, it is true to say that the surface microlayer, which today is inhabited by the neuston, would probably have been a particularly extreme environment. Below a 30-m depth, UV radiation would have been

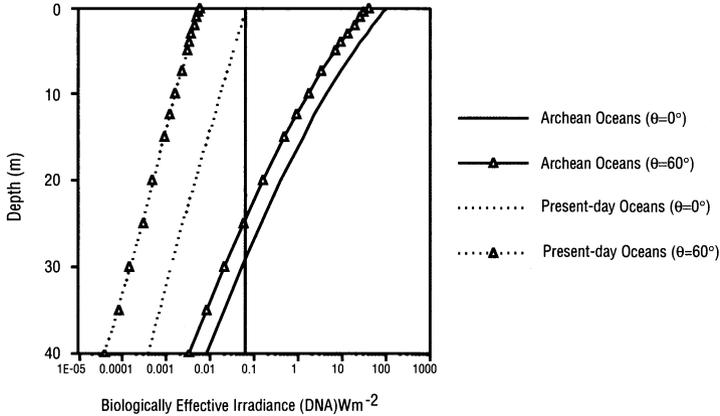


FIGURE 1.4. DNA-weighted irradiance penetrating into the Archean oceans (same atmospheric assumptions as in Figure 1.3 and at $\theta = 0^\circ$ and $\theta = 60^\circ$). The vertical line from the surface is the value of present-day DNA-weighted irradiances at $\theta = 0^\circ$. It gives an indication of the depth at which DNA-weighted irradiances would be the same as the exposed surface of present-day Earth.

significantly reduced, but PAR would have been one to two orders of magnitude higher than the light saturation points of many present-day phytoplankton (Kirk 1994). A deep chlorophyll maximum of high photosynthetic productivity could have existed in the Archean as it does today (Garcia-Pichel 1998; Cockell 2000b). Thus, the stratified oceans that some envisage in the Precambrian (Chamberlain and Marland 1977) are not prevented from being inhabited by photobiological considerations.

Intertidal and Terrestrial Habitats

In examining a range of physical and biological screening methods, Cockell (1998) concluded that there are a wide variety of substrates that can provide reduction of DNA-weighted irradiances of more than two orders of magnitude. Under such substrates, Archean organisms could be exposed to DNA-weighted irradiances similar to an exposed organism on present-day Earth. Because we know a diversity of single-celled organisms exist in exposed habitats today, such as, for example, the neuston that inhabit the microlayer of the oceans, then it is apparent that survival and growth under even the worst UV estimates for the Archean is likely to be possible with appropriate strategies. Admittedly, even exposed single-celled neuston produce UV-screening compounds. Therefore, the comparison between biologically effective irradiances achieved by hiding under substrates and the full exposed value on present-day Earth is not entirely accurate. However, it suffices in that here we are considering order-of-magnitude reductions that many of these substrates do 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 some organisms (Nienow, McKay and Friedman 1998), such as the primitive cyanobacterium *Chroococcidiopsis*, are still able to photosynthesize. These reductions are sufficient to reduce UV irradiances from values experienced on the Archean Earth down to values well below those in exposed regions today.

Reduced ferrous iron, which would have been upwelled from the deep anoxic Archean oceans, may also have protected some organisms (Olson and Pierson 1986; Garcia-Pichel 1998). As suggested earlier, it could have been stripped from the water by an oxidized upper layer. Although it would therefore have precipitated from the surface layers in the oceans, providing limited UV protection, in intertidal regions it could have precipitated directly onto intertidal communities as ferric iron, providing some protection.

Sediments themselves can provide UV protection. DNA-weighted irradiances would be reduced to present-day exposed values within the first few millimeters. Garcia-Pichel and Bebout found that UV-B was reduced to 1% between 1.25 and 0.23 mm from the surface (Garcia-Pichel and Bebout 1996). In some sediments such as carbonate sands, UV-B radiation was found to be higher in the very near surface environment because of light-trapping effects. Nevertheless, it is clear that sedimentary layers would have been an effective strategy for a microbial benthos.

Protection of organisms may be enhanced by the matting habit, whereby the upper layer of dead organisms protects organisms underneath by virtue of their UV-screening compounds. Margulis et al. (1976) 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 (Walter 1983). Indeed, it is probably the only UV protection strategy that we can truly support with confidence based on real fossil record evidence.

Other less commonly distributed strategies could have existed. For example, even thin layers of elemental sulfur will absorb UV radiation in the UV-C and UV-B regions (Cockell 1998). Some microbial mats near hot springs become covered in thin layers of sulfur (Castenholz, Bauld and Jorgensen 1990). It is plausible that organisms with sufficient sulfur coverings in solfatara fields could acquire UV protection. Table 1.2 lists a diversity of potential protection mechanisms with their possible locations on early Earth.

Ultraviolet Radiation-Screening Compounds

The disadvantage of many of these substrates is that they also absorb photosynthetically active radiation (PAR). This absorbance is not a concern for organisms that compete by slow persistent growth, such as some cyanobacteria. However, for many organisms such as those that inhabit the oceanic photic zone, there may