

Constraints on a potential aerial biosphere on Venus: II. Ultraviolet radiation

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ABSTRACT

Despite the harsh conditions in the atmosphere of Venus, the possibility for an aerial habitable zone exists. A thermal habitable zone is predicted to exist at an altitude range of 62 to 48 km, above which temperatures drop below the lower thermal limit of cell growth and below which temperatures exceed the evaporation temperature. Many biocidal factors must be considered for the complete definition of an aerial habitable zone; in this study we consider the constraint specifically from the perspective of biocidal solar ultraviolet (UV) intensity in the atmosphere. We simulated the penetration of solar ultraviolet and visible light through the atmosphere using a radiative transfer model, to determine the spectral environment (and thus the UV biocidal effect) as a function of altitude in the atmosphere of Venus. At the top of the thermal aerial habitable zone (62 km) the incoming solar irradiance creates a severely challenging UV environment, with extremophiles such as *Deinococcus radiodurans* expected to be able to endure these UV conditions for approximately 80 s. At an altitude of around 59 km the biologically-weighted UV irradiance drops below that calculated for the Archean Earth, and continues to fall with decreasing altitude until at 54 km it is less than that found currently at the surface of Earth. Crucially, longer wavelength photosynthetically active light continues to penetrate to these altitudes and below, resulting in a solar radiation environment in the venusian atmosphere below around 54 km that screens biologically-damaging UV radiation yet permits the process of photosynthesis. Whilst not claiming to suggest the existence of an aerial habitable zone in general, by considering thermal conditions, ionising radiation and the UV flux environment of the venusian cloud deck alone, we define a potential habitable zone that extends from 59 km to 48 km. This region should form the focus of future remote and in situ astrobiological investigations of Venus.

1. Introduction

Venus and Earth share several similarities, yet the evolution of their planetary environments have followed distinctly different evolutionary paths (e.g. Walker, 1975; Kasting, 1988; Svedhem et al., 2007; Driscoll and Bercovici, 2013) leading to two very different environments in the context of potential habitability. The high pressure, high temperature conditions on the present-day surface of Venus are known to preclude the presence of liquid water, thus making the surface inhospitable to life as we know it. It has been proposed that the surface of early Venus may have been habitable and hosted a significant abundance of liquid water (Kasting, 1988; Donahue and Hodges, 1992; Kulikov et al., 2006; Barabash et al., 2007). Over time, this water was lost from the surface as the

rising temperatures lead to evaporation into the atmosphere. This atmospheric water vapour would then have been readily dissociated by solar UV photolysis, and the resulting ions free to escape to space and be stripped away from the planet by the solar wind (Barabash et al., 2007; Dubinin et al., 2011). Although previous studies concluded that such escape processes could have driven considerable loss of H and O over planetary history (Chassefière et al., 2012), Persson et al. (2020) have recently argued from measurements by Venus Express that present-day escape rates cannot account for the loss of a past Earth-like ocean. However, the possibility remains that the Venus provided an early environment sufficiently clement and long-lived (Kasting, 1988; Grinspoon and Bullock, 2003; Way et al., 2016; Way and Del Genio, 2020), for life to have originated. Alternatively, such an early habitable surface

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environment could have been colonized through lithopanspermia by microbes transferred from Earth by meteorite impacts (e.g. Melosh, 1988; Worth et al., 2013).

As conditions for stable liquid water migrated from the surface into the atmosphere, the location of the venusian ‘habitable zone’ would have moved along with it towards the clouds. Thus, in order to assess the feasibility of present-day life on Venus, the habitability of the venusian clouds must first be quantified and explored from multiple perspectives.

1.1. The potential for life in the clouds

Given the present-day thermal environment of Venus, the cloud decks represent the only reservoir for liquid water, a critical requirement for habitability. The potential for an aerial biosphere on Venus within this environment has been established by several studies (Sagan, 1961; Morowitz and Sagan, 1967; Grinspoon, 1997; Cockell, 1999; Schulze-Makuch and Irwin, 2002; Limaye et al., 2018; Seager et al., 2020; Limaye et al., 2021) and a summary of this context can be found in the companion paper to this study (Dartnell et al., 2015). The water in the venusian clouds is primarily within H₂SO₄-bearing aerosol droplets (Young, 1974), and therefore, this environment is far from benign. Earlier theoretical assessments of the pH levels encountered in the cloud droplets indicated that it could range between pH 0.5 in the upper clouds to pH -1.3 in the lower cloud region (Grinspoon and Bullock, 2007), which compares favourably with the known survivability of terrestrial acidophiles. However, when employing the Hammett acidity value appropriate for very concentrated solutions of sulphuric acid, Seager et al. (2020) calculate the Hammett Acidity (H_0) of the venusian clouds to be about -11.5. The environmental conditions within the venusian clouds are orders of magnitude more acidic and more arid than any natural environment on Earth, and beyond the survival limits of any known terrestrial extremophile organism (Seager et al., 2020). The plausibility of a venusian aerial biosphere may require the existence of cellular mechanisms unknown in terrestrial biology that enable survival in extremely acidic environments, however, it is noted that less acidic cloud droplets have been proposed by Rimmer et al. (2021) and a study published during the review of this publication casts doubt on the available water within aerosol droplets in Venus’ clouds (Hallsworth et al., 2021).

Highly acidic conditions are very damaging to the complex molecules of life, and terrestrial acidophiles employ both passive and active mechanisms to maintain the internal environment of their cytosol at much closer to neutrality, as well as rapidly repairing damage as it occurs. These adaptations include a more impermeable cell membrane, cytosolic buffering molecules, maintaining a reversed membrane potential (i.e. concentrating positive-charged ions inside the cell) to impede proton influx, active proton pumping, and large numbers of DNA repair enzymes and protein re-folding chaperones to rapidly and efficiently repair biomolecule damage caused by low pH (Baker-Austin and Dopson, 2007). Putative venusian microbes may be expected to exploit similar strategies to tolerate the extreme acidity of the cloud droplets.

Such active mechanisms for survival under acidic conditions are energetically expensive. For example, an acidophilic unicellular green algae *Chlamydomonas* sp. isolated from Rio Tinto acid mine drainage system was found to consume 7% more ATP per second at pH 2 than pH 7 due to removal of protons entering the cytosol across a permeable cell membrane (Messerli et al., 2005). Bethmann and Schönknecht (2009) found that for the acidophilic unicellular green algae *Eremosphaera viridis* more than 50% of the ATP budget was used for proton pumping to control the cytosolic pH. In addition to active mechanisms for surviving the extreme acidity, venusian microbes would also need to actively pump water molecules into the cell from the concentrated sulphuric acid of the droplet around them, as well as other nutrients against their concentration gradient, and, without interaction with the planetary surface, fix gaseous elements from the atmosphere. In sum, survival in the venusian clouds would be very energetically intensive (see Cockell

et al. (2021) for a detailed discussion of energetics).

Potential sources of energy for metabolic processes within the atmosphere of Venus include chemotrophic reduction of sulphates (Cockell, 1999; Schulze-Makuch et al., 2004), but the energetic costs of survival and paucity of redox disequilibria available to microbes within cloud droplets imply that venusian aerial life must be photosynthetic (Seager et al., 2020), possibly absorbing ultraviolet wavelengths, and employing the oxidation of hydrogen sulphide or carbonyl sulphide (Schulze-Makuch et al., 2004). Recently, Greaves et al. (2020) announced the detection of phosphine in the venusian atmosphere at levels they argued is orders of magnitude higher than can be accounted for by known abiotic chemical processes. This would imply the existence of either some as-yet unknown abiotic chemical reaction pathway operating under the extreme venusian atmospheric conditions, or potentially is a sign of biochemistry occurring within an aerial biosphere. While both the claimed detection of phosphine and, if present, its source are still contested (Mogul et al., 2020; Thompson, 2020; Greaves et al., 2020b; Greaves et al., 2020c; Lincowski et al., 2021; Villanueva et al., 2021; Greaves et al., 2021), it remains a potential biosignature. This begs the question: if microbial life is present on Venus, where in the atmosphere would it be found?

From a consideration of temperature alone, the potential ‘thermal habitable zone’ on Venus would be defined by the altitude range that corresponds to the temperature range of growth for known extremophilic microorganisms: ~120 °C to -20 °C (Cavicchioli, 2002). Some authors (e.g. Cockell, 1999) have argued for an upper temperature limit as high as 150 °C, determined by the stability of complex organic molecules. However, as we argue in Dartnell et al. (2015), the combined effects of high temperature and high acidity are extremely destructive to organic molecules, and terrestrial polyextremophile organisms able to tolerate these concurrent environmental challenges (thermophilic hyperacidophiles) cannot survive pH 0 at temperatures higher than 65 °C. Given that any putative venusian life would in any case need to be able to survive acidities greater than any known terrestrial acidophile (Seager et al., 2020) we define here the venusian habitable region between the lower thermal limit of -20 °C and the base of the lower cloud region, below which liquid droplets will have evaporated. Fig. 1 plots the temperature and pressure profiles through the venusian atmosphere (data from Venus International Reference Atmosphere: Kliore et al., 1985; Seiff et al., 1985; Keating et al., 1985), and so shows that these limits would place the habitable region between 47.5 km (around 100 °C) and 62 km (-20 °C) above the surface, an altitude range over which the pressure regime is also benign to life. This potential habitable zone is indicated in Fig. 1 (and subsequent results Figures in this paper) as a green band.

Clouds on Venus represent an optically thick, ubiquitous feature of the atmosphere, with the small aerosols remaining suspended in the atmosphere for periods of months at a time. These aerosols therefore represent potential micro-environments that could remain stable for significant periods provide an aerial habitable zone (HZ) (Grinspoon, 1997; Schulze-Makuch et al., 2013). As a possible solution to the problem of how a venusian biosphere could have remain lofted in the atmosphere for hundreds of millions or even billions of years, Seager et al. (2020) propose a microbial life cycle linked to vertical circulation. Cloud droplets containing cells grow and then settle under gravity into the deeper, hotter atmosphere. During this descent, the droplets evaporate, and the microbes produce desiccated spores, resistant to environmental stresses. Thus, they argue, there could be a depot of dormant life in the lower haze layer. Spores are returned to the cloud layer by upwelling caused by gravity waves, act as cloud condensation nuclei to become rehydrated, germinate back into a metabolically active state and continue the life cycle.

1.2. Ultraviolet radiation

Lofted around 48–62 km high in the atmosphere, the potential

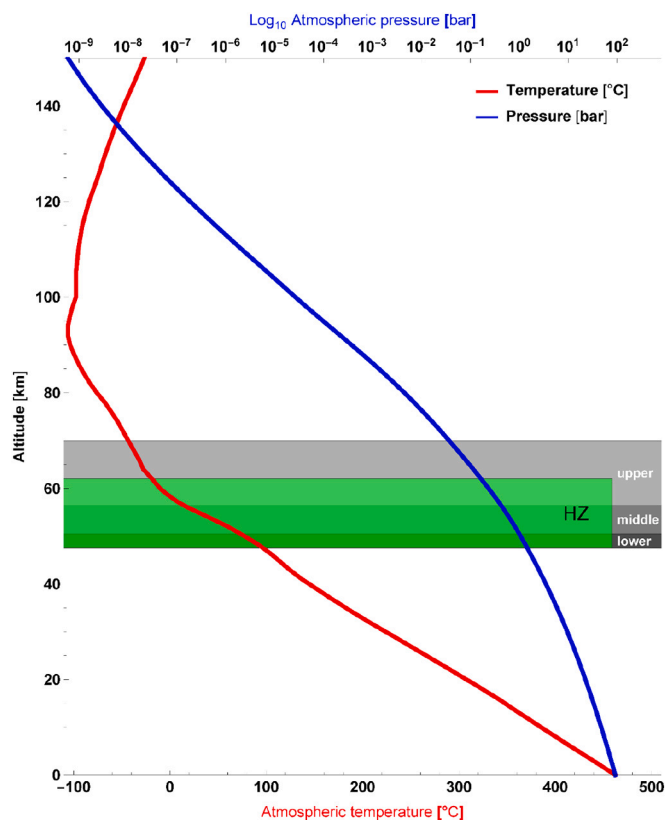


Fig. 1. The altitude range of the thermally-defined habitable zone in the Venusian atmosphere. Temperature (red) and pressure (blue) are plotted as a function of altitude. The three main cloud regions of Venus are shown in shades of grey and the aerial habitable zone, bounded by a temperature of -20°C (62 km) and the base of the lower cloud level (47.5 km), is indicated by the green band (labelled HZ). Updated from [Dartnell et al. \(2015\)](#). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

habitable zone may be expected to be exposed to much higher levels of radiation from space than the terrestrial biosphere ([Dartnell et al., 2015](#); [Herbst et al., 2019](#)). The companion paper to this present one, [Dartnell et al. \(2015\)](#) modelled the propagation of solar energetic particles and galactic cosmic rays through the upper atmosphere; and here we consider the penetration of solar ultraviolet radiation into the aerial habitable zone.

Many biomolecules are susceptible to degradation by ultraviolet radiation, which is commonly subdivided into three spectral regions: UVA (400–315 nm), UVB (315–280 nm) and UVC (280–~180 nm) ([Castenholz and Garcia-Pichel, 2012](#)). UVB and UVC wavelengths are strongly absorbed by the pi-electron systems present in aromatic and indolic structures such as that of the nucleobases in DNA and RNA, or the amino acids tryptophan, tyrosine and histidine in proteins, as well as the conjugated structures of unsaturated aliphatic molecules like the fatty acids and lipids of cell membranes ([Cockell, 1999](#)). UVC and UVB radiation therefore results in DNA lesions and protein damage, including photosystems, and is very deleterious to cellular survival. Longer wavelength UVA also inhibits photosynthesis, is absorbed by and can directly damage essential nucleotide cofactors such as NAD(P)H, and in the presence of free oxygen (not so much in the case of Venus, but such as on the contemporary terrestrial surface) UVA photochemistry drives the production of reactive oxygen species such as singlet oxygen and various free radicals which causes indirect damage to a wide range of a cell's biomolecules ([Dillon et al., 2002](#); [Castenholz and Garcia-Pichel, 2012](#)).

A terrestrial cell exposed to short wavelength UV radiation thus

suffers DNA lesions and damage to its proteins and photosystem (if present), which are extremely deleterious to survival. Even if life on Venus (or elsewhere) were not based on precisely the same biomolecules as terrestrial biology – DNA/RNA, proteins, lipid bilayers – it can be presumed to require complex organic chemistry, including many biomolecular moieties containing pi-electrons, and so be vulnerable to ultraviolet radiation ([Cockell, 1998](#)). It is for this reason that modelling studies on the biological effects of UV radiation on a given biomolecule or organism often employ an empirical action spectrum, which gives the relative biological response as a function of wavelength ([Horneck, 1995](#); [Cockell, 2000](#)). The product of the UV spectrum and the action spectrum yields the biologically effective irradiance (see Methods for more details).

Terrestrial life exploits many protective strategies to survive ultraviolet irradiation, and, indeed, life on Earth emerged at least 3.5 billion years ago during the Archean era when there was no atmospheric ozone layer to shield the surface from high solar UV flux. These survival strategies include:

- (i) synthesising UV-screening compounds such as scytonemin or mycosporin and mycosporin-like amino acids ([Cockell and Knowland, 1999](#); [Balskus and Walsh, 2010](#));
- (ii) forming microbial mats whereby the lower layers are protected by the UV absorption or scattering of the upper layers ([Ehling-Schulz and Scherer, 1999](#));
- (iii) colonising natural habitats that provide UV protection, such as living hypolithically underneath translucent stones or endolithically within cracks and pore-spaces of rocks ([Friedmann, 1986](#));
- (iv) or simply beneath a sufficiently deep water column to shield UV ([Booth and Morrow, 1997](#); [Cleaves and Miller, 1998](#)).
- (v) Once caused, the cell can also attempt to actively repair UV damage using, for example, enzymatic DNA repair mechanisms and de novo re-synthesis of proteins and lipids ([Cockell, 1999](#); [Ehling-Schulz and Scherer, 1999](#))

While possible life within aerosol droplets suspended high in the Venusian atmosphere may well produce UV-screening compounds, the other protective strategies – forming microbial mats on a substrate, or exploiting the UV ameliorating effects of minerals or water – are clearly not available. Previous commentators (e.g. [Cockell, 1999](#)) have assumed that UV radiation in the Venusian clouds is likely not prohibitive to life because the UV flux at higher altitudes is comparable to that on the surface of archaic Earth when photosynthetic life thrived, with higher UV levels even possibly playing a role in the establishment of life ([Patel et al., 2015](#)). One aspect that is not often considered, however, is the consideration that early terrestrial life may have utilised UV-shielded habitats that are not feasible in a potential Venusian biosphere. The UV spectrum through the Venusian atmosphere is therefore of prime concern for the potential habitability of this aerial region ([Schulze-Makuch et al., 2004](#)).

Previous studies have considered the impact of stellar UV radiation on potentially habitable bodies in the context of astrobiology. These include modelling the UV spectrum on the surface of Mars under both current and modelled ancient atmospheric conditions ([Cockell et al., 2000](#); [Ronto et al., 2003](#); [Patel et al., 2004a](#); [Patel et al., 2004b](#); [Cordoba-Jabonero et al., 2005](#); [Ranjan et al., 2017a](#)); or the Earth at different epochs in its planetary evolution, such as the Archaean when life developed but there was no protective ozone layer ([Cockell and Raven, 2004](#); [Clossen et al., 2007](#); [Ranjan and Sasselov, 2017](#)); or for terrestrial exoplanets orbiting within the habitable zone of different categories of stars ([Segura et al., 2003](#); [Sato et al., 2014](#); [Rugheimer et al., 2015](#); [Ranjan et al., 2017a, 2017b](#); [O'Malley-James and Kaltenegger, 2019](#)). [Cockell \(2000\)](#) used a single scattering carbon dioxide-nitrogen atmosphere model to calculate the UV flux onto the Venus surface over planetary history and found that the flux rapidly reduces as the increasing atmospheric pressure exceeds 10 bar, and found the flux

at the surface to be negligible as the pressure approaches the present-day value of 90 bar. However, to date there have been no detailed estimates of UV flux transmission through the venusian atmosphere.

Here we present the first results of the modelled UV radiation environment as a function of altitude through the potential venusian aerial habitable zone.

2. Method

2.1. Model description

We have utilised a radiative transfer model originally developed for the martian atmosphere (Patel et al., 2002) adapted to the conditions of the Venus atmosphere. Details of the method can be found in Patel et al. (2002, 2004a, 2004b) and are summarised here for clarity including the adaptations for Venus implementation. We use a two-stream delta-Eddington approximation to compute the upwards and downwards radiative transfer through 71 plane-parallel layers, each 2 km thick and homogeneous, to represent the Venus atmosphere from the surface to the top of the atmosphere. No pseudo-spherical correction is required since we do not consider cases of large solar zenith angles. The overall optical depth, single scattering albedo and asymmetry parameter are defined for each layer, considering the gaseous and aerosol contribution to each of those elements. We consider the radiative transfer through these layers incorporating absorption and multiple scattering over the wavelength range 180–600 nm. Thermal emission is not accounted for in our radiative transfer process since thermal emission at UV wavelengths is negligible with respect to the UV insolation under these conditions. For each layer, we consider the radiative effects of gases and cloud aerosols in the atmosphere of Venus. Gaseous extinction is accounted for the following gases: CO₂, N₂, CO, SO₂, SO, H₂O, OCS, HCl and HF (Section 2.3). The Rayleigh scattering cross-section is calculated for each species, defining the scattering contribution to the extinction cross section. Laboratory measurement values from the literature are used to define the absorption cross-section of each molecule, and where no absorption cross-section data are available, the absorption cross-section value at these wavelengths is set to zero (in these cases, only the Rayleigh scattering contributes to extinction). The optical depth contribution is then calculated considering the combination of the extinction cross-section and the layer column abundance of each species. Aerosol scattering is accounted for by considering the Mie scattering from the cloud particles (mode 1–3 particles) using the optical properties shown in Fig. 6 (see Section 2.4). We employ a thermal structure for the Venus atmosphere described by Haus et al. (2013) to determine the pressure (and thus species abundance) in each model layer assuming

hydrostatic equilibrium. The resulting pressure profile is shown in Fig. 2.

2.2. Solar spectrum

We use the ASTM E-490 Air Mass Zero (AM0) Standard Spectra (ASTM E490-00a (2014)) corrected for the Sun-Venus distance as our input solar irradiance, Fig. 3 The ASTM E490 AM0 solar irradiance is a collation of data from satellites, space shuttle missions, high-altitude aircraft, rocket soundings, ground-based solar telescopes, and modelled spectral irradiance. The UV (200-400 nm) irradiance at the top of the Venus atmosphere is $\sim 200 \text{ W m}^{-2}$, which is approximately twice that at Earth and follows the inverse square law for Venus' average distance of 0.72 AU. Half of the UV radiation incident on Venus is absorbed at the cloud tops ($\sim 65 \text{ km}$) by SO₂, SO and the unknown UV absorber. The upper cloud structure and the abundances of the absorbing species are highly variable, causing albedo variations of up to 30% and resulting in the UV absorptions that are pronounced in global observations of Venus (e.g. Titov et al., 2007).

2.3. Atmospheric composition

The atmosphere of Venus comprises predominately of carbon dioxide (CO₂) with the other major gas being nitrogen (N₂) and contains numerous trace gases that include SO₂, SO, HCl, CO, and O₃. The vertical profiles of SO₂ retrieved by Sandor et al. (2010) in the sub-mm range from the James Clerk Maxwell Telescope and by Belyaev et al. (2012) from SOIR and SPICAV-UV occultation observations show two distinct layers of SO₂ in the Venus mesosphere. A lower layer (60–85 km) which shows a decrease in SO₂ concentration with altitude, due to photodissociation by incident UV radiation, and an upper layer (85–105 km) characterised by a significant increase in SO₂ with altitude from 0.05 ppmv at the base to 0.2 ppmv at the top. A possible source of SO₂ in the upper layer could be photo-dissociation of H₂SO₄ vapour, resulting from the evaporation of the acid aerosol particles, producing H₂O and SO₃. The SO₃ can be broken down further by light to produce SO₂ and O (Zhang et al., 2010; Zhang et al., 2012). The gaseous abundances and vertical profiles relevant to this study are shown in Fig. 4 between 0 and 80 km and were taken from Tsang et al. (2008). The SO₂ mixing ratio above 85 km was taken from Fig. 4 in Belyaev et al. (2012) to account for the mesospheric SO₂ layer. It should be noted that the abundance of SO₂ in the atmosphere of Venus varies considerably with location and time (e.g. Vandaele et al., 2017a, 2017b; Encrenaz et al., 2019; Marcq et al., 2020; Shao et al., 2020; Evdokimova et al., 2021), as well as that of OCS (e.g. Krasnopolsky, 2010; Krasnopolsky, 2012; Rimmer et al., 2021). In this study, we aim to investigate a generalised representation of the

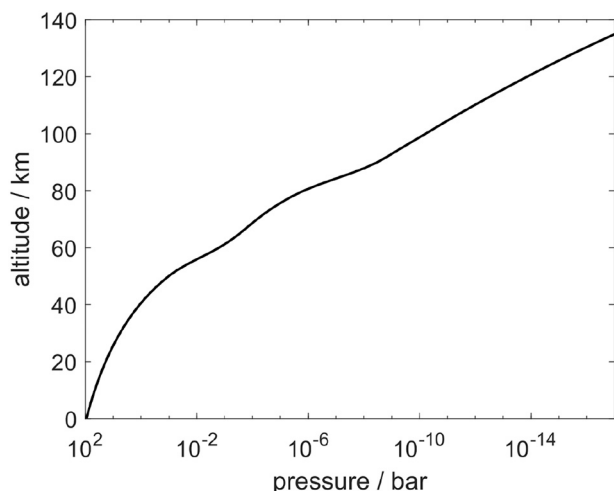


Fig. 2. Pressure-altitude profile used in the radiative model.

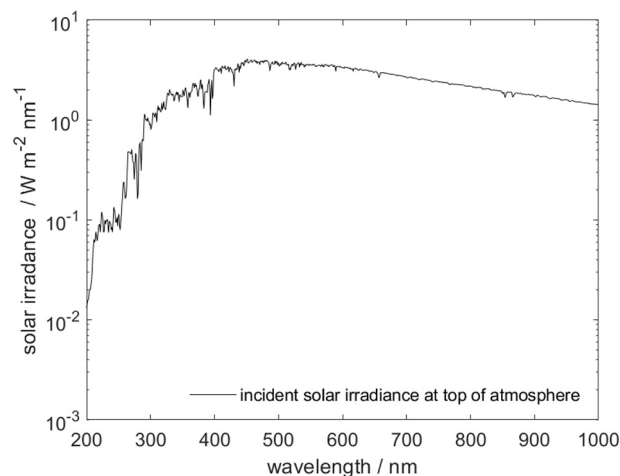


Fig. 3. Solar irradiance incident at the top of the Venus atmosphere. (ASTM E490-00a, 2014).

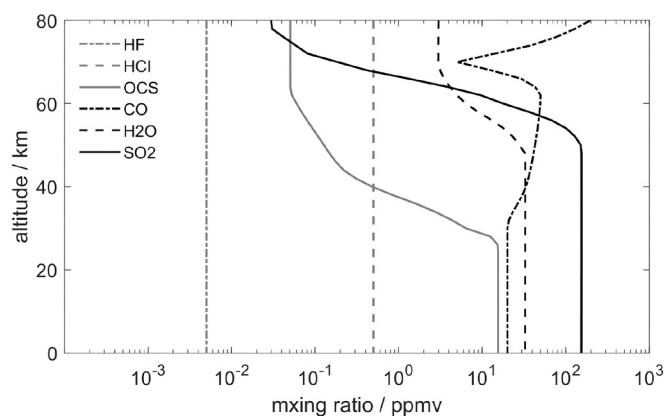


Fig. 4. The vertical distribution of the trace gases in the Venus atmosphere (Tsang et al., 2008).

atmosphere of Venus covering several gases, hence the use of the Tsang et al. (2008) profiles. Assessment of the spatiotemporal variation of the UV spectral environment for Venus at a global level is beyond the scope of this work but the inherent variability in species abundances should be considered in the interpretation of the results presented in this paper. The amount of CO_2 and N_2 are fractional abundances of 0.965 and 0.035 respectively and assumed to be vertically uniform. HCl is a minor trace gas in the Venus atmosphere, however, it is active in the UV in the wavelength range 100–240 nm and the vertical mixing ratio is assumed constant with altitude in this study (Connes et al., 1967; Bézard et al., 1990).

The Venus atmosphere is dominated by thick aerosol clouds that are made of small droplets of sulphuric acid of concentration 75–90% in H_2O . The vertical structure of the clouds was measured by the Venera 1 and 2 descent probes and analysis of the data revealed a three layer cloud structure with the base of the lower layer at around 48 km, the middle layer at 60 km and the top layer starting at about 70 km (Tomasko et al., 1980; Seiff et al., 1980). A light haze of variable optical thickness exists beneath the cloud layers and also in the mesosphere (Crisp, 1986). General agreement between radiative models and the Venera descent probes has been accomplished by describing the clouds using four size ranges, known as ‘modes’; mode 1, mode 2, mode 2’ and mode 3 for the aerosols (Tomasko et al., 1980; Crisp, 1986). In this study the vertical distributions of the four aerosol modes were taken from Haus et al. (2015) and are shown in Fig. 5. The mode 1 component is present in all cloud regions and consists of the smallest submicron size particles. Mode 2 and mode 2’ are micron sized particles with mode 2 dominant in the upper cloud while mode 2’ is confined to the lower cloud region along with the largest particles described by mode 3. We

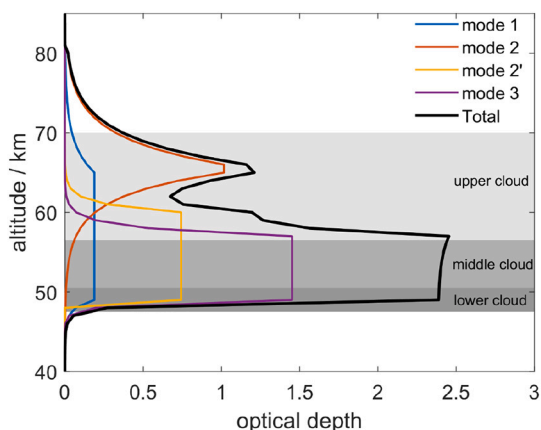


Fig. 5. Vertical structure of the venusian H_2SO_4 clouds (Haus et al., 2015).

note the variable presence of condensed sulfur occurring as potential scattering aerosols which have been studied in detail previously (e.g. Zhang et al., 2012), however given that we only consider a generalised global representation here, we do not explicitly model the contribution to scattering of the varying presence of condensed sulfur.

2.4. Aerosol optical scattering and the UV absorber

At visible wavelengths the cloud aerosol albedo is very high with approximately 85% of the solar light incident at the cloud tops being scattered back into space. Spectroscopic measurements have provided strong evidence that the chemical composition of the mode 2 aerosol particles corresponds to liquid sulphuric acid (Crisp, 1986; Tomasko et al., 1985), however the exact composition of the mode 1 and mode 3 particles is still being debated (Taylor, 2006). We follow the previous studies and extend the mode 2 composition to encompass all modes and use log normal distributions to describe all four aerosol modes with the modal radii and unitless dispersions given in Table 1. The complex refractive indices of 75% solutions of H_2SO_4 in H_2O taken from Palmer and Williams (1975) and Mie theory (Wiscombe, 1980) are used to determine the wavelength-dependent extinction and scattering cross-sections and asymmetry parameter for the aerosols (shown in Fig. 6), as well as the single scattering albedo which has a value of unity across the wavelength range considered here.

Observations of the venusian atmosphere have detected the presence of an unknown UV absorber at wavelengths shorter than 600 nm (Rossow et al., 1980; Moroz et al., 1983). The UV absorber is situated in the upper cloud, however the exact abundance and composition of the aerosol has remained elusive and debated for many years. Recent results have proposed candidates for the UV absorber, such as the S_2O_2 isomers, *cis*-OSSO and *trans*-OSSO (Frandsen et al., 2016), or FeCl_3 (Krasnopolsky, 2017) but the UV optical constants of these condensed species are not experimentally well-constrained. More detailed observations of this region of the spectrum are required to settle the debate on the species responsible. It is believed that this absorber is responsible for the majority of the sunlight absorbed in the atmosphere of Venus above 60 km (Economov et al., 1983; Pollack et al., 1980; Tomasko et al., 1980; Crisp, 1986; Krasnopolsky, 2006). The lower extent of this absorbing layer was constrained by the solar flux radiometer experiment on the Pioneer probe (Tomasko et al., 1980) which shows little to no absorption below 57.5 km; the upper extent of the UV absorbing layer is less constrained. Since the exact composition and absorption properties of the UV absorber remains unknown, the absorber has previously been modelled by reducing the single scattering albedo of mode 1 aerosol particles between 56 and 70 km in the 300–780 nm spectral range until their simulated spectra agreed with the Venera 11 descent data (Tomasko et al., 1980; Pollack et al., 1980). This assumption was used in other investigations (Toon et al., 1982; Crisp, 1986) and is supported by the observed correlation between the vertical distribution of the UV absorber and the mode 1 particles in the upper cloud. An alternative method, proposed by Haus et al. (2015) and adopted here, was to describe UV absorber simply as an opacity source and adjust the absorption cross-section of the UV absorber until the modelled planetary albedo agreed with observational measurements. In this manner, the radiative effect of the unknown absorber can be accounted for, without needing to define its chemical properties. The subsequent wavelength dependent absorption cross-section for the UV absorber used in this study as derived by Haus et al. (2015) is shown in Fig. 7, as well as its

Table 1

Modal radii and dispersion for the aerosol log-normal distributions (Pollack et al., 1993).

Mode	1	2	2'	3
Radius	0.3	1.00	1.40	3.65
Sigma	1.56	1.29	1.23	1.28

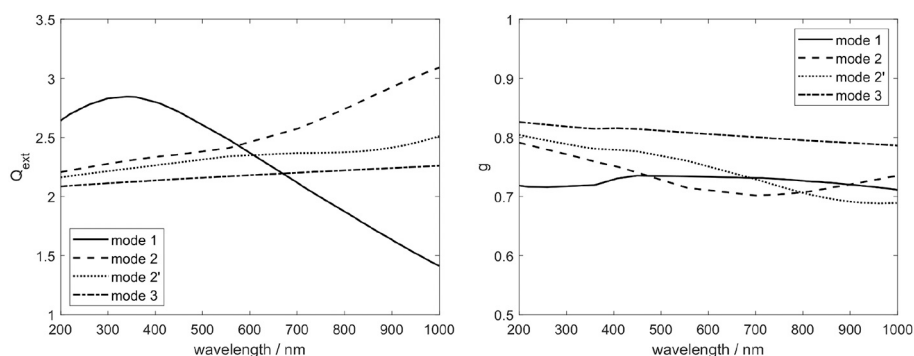


Fig. 6. (left) The extinction efficiency of mode 1, mode 2, mode 2' and mode 3 H_2SO_4 aerosol particles. (right) The asymmetry parameter (g) of mode 1, mode 2, mode 2' and mode 3 H_2SO_4 aerosol particles. The single scattering albedo is constant at a value of 1 across these wavelengths.

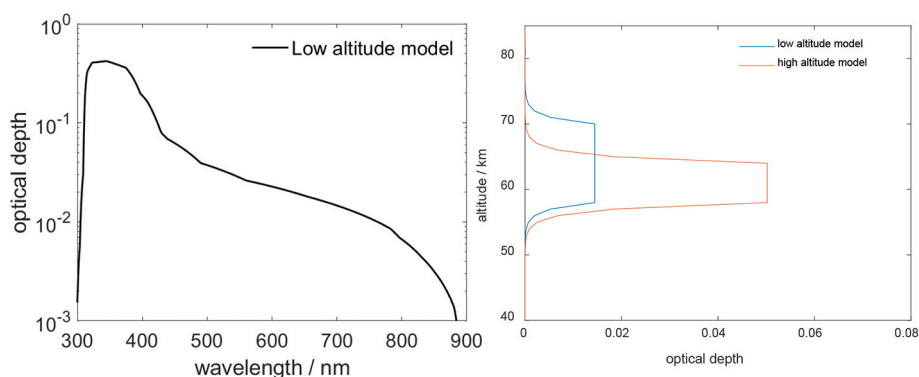


Fig. 7. (left) The wavelength dependent absorption cross-section of the unknown UV absorber (Haus et al., 2015). (right) The vertical distribution of the unknown UV absorber (Haus et al., 2015).

vertical distribution which was assumed to follow the low altitude model description from Haus et al. (2015).

2.5. Biological weighting

Different wavelengths of ultraviolet radiation are not uniformly harmful to microorganisms. The exact wavelength dependence is determined by the molecular target and biological outcome (such as DNA damage and cell death, or photosystem inhibition) and can be represented as an action spectrum, i.e. the relative biological effectiveness as a function of UV wavelength. For terrestrial microorganisms, DNA damage and loss of cellular viability is the major outcome of UV radiation damage, and so the DNA action spectrum is widely used for the biological assessment of UV radiation in both terrestrial and martian studies (e.g. Cockell et al., 2000; Patel et al., 2004a, 2004b; Cordoba-Jabonero et al., 2005). Here, we use the generalised DNA action spectrum shown in Fig. 8, derived by Cockell (1999) by combining the DNA absorbance spectrum between 200 and 280 nm (Horneck, 1993) with the standard DNA action spectrum for wavelengths longer than 280 nm (Green and Miller, 1975). Ideally, a standard action spectrum would be used <280 nm, but due to the lack of action spectrum data at these wavelengths, the approach of Cockell (1999) is deemed appropriate for this general analysis of model organism response. A factor $\times 2$ increase in fluence <280 nm results in a factor $\times 1.83$ increase in DNA-weighted dose at 60 km, and this potential sensitivity should be considered when interpreting the results presented in this study. The lack of a DNA action spectrum standard for wavelengths <280 nm is a significant weakness given the strong dependence on radiation at these wavelengths. Measurements of the DNA action spectrum at these wavelengths would be of great benefit to the community, for analyses such as presented here. Putative venusian microbial life may also employ DNA due

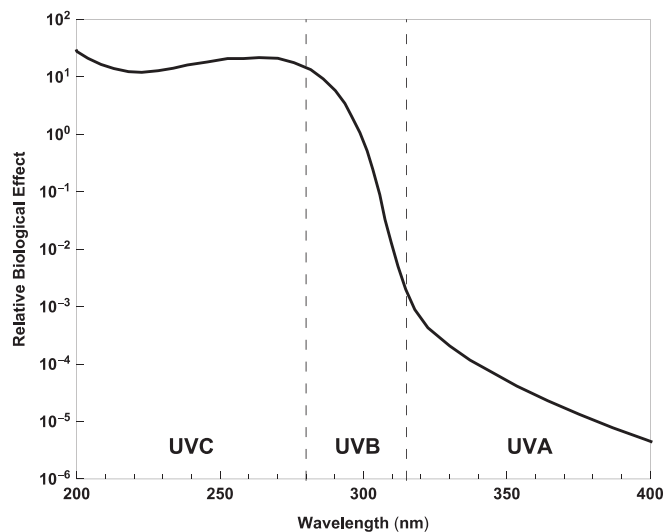


Fig. 8. The action spectrum used to calculate biologically effective UV irradiance, based on that for DNA presented in Cockell (1999), normalised to 300 nm.

to common descent and interplanetary transfer between Earth and Venus by lithopanspermia during the Late Heavy Bombardment, or convergence of biomolecular systems in the case of an independent origin of life. In any case, this generalised action spectrum is taken to be representative for any microorganism whose genetic material and enzymes use UV-absorbing moieties such as aromatic and indolic molecular structures.

The convolution of this action spectrum with the modelled UV flux

spectrum at any given altitude in the venusian atmosphere yields the biologically effective spectral irradiance. Numerically integrating this spectrum gives the biologically effective UV total irradiance.

3. Results and discussion

Here we present the results of the radiative transfer modelling simulations, to determine the spectrum and integrated irradiance through the atmosphere down to a lower altitude of approximately 40 km, just beyond the lower altitude of the defined HZ.

3.1. Spectrum and integrated irradiance vs. altitude

Fig. 9 focusses on a subset of all the irradiance spectra (i.e. the sum of the downwelling and upwelling flux) produced by this study, showing the solar spectrum entering the top of the atmosphere (140 km) and the spectra modelled at regular altitudes through the aerial habitable zone. These are compared against spectra calculated elsewhere for the present-day Earth surface and Archean Earth surface (3.9 Gya, before the formation of the ozone shield; Ranjan and Sasselov, 2017) and the martian surface (Patel et al., 2004a, 2004b). Fig. 9 shows that the UV radiation environment around 60–62 km altitude in the venusian atmosphere, at the top of the habitable zone, is similar to that of the martian surface, with a considerable irradiance of UVC still penetrating. At 58 km altitude significant absorption of UVC-UVB wavelengths around 280 nm occurs due to the increase in sulfur species abundance and Rayleigh scattering, and by 56 km altitude there is a similar UVA spectral cut-off to the Earth's surface at sea level, but with a small peak at around 240 nm. At 54 km, there is no UVB or UVC light present. Comparing to results from Zhang et al. (2012), who presented results at 112, 70 and 58 km, we see a generally good agreement at 112 and 70 km, where the vertical profile of gases and aerosols is relatively smooth. At 70 km, Zhang et al. (2012) calculate an irradiance at 300 nm of $\sim 0.1 \text{ W m}^{-2} \text{ nm}^{-1}$, compared to this study with a value of $\sim 0.4 \text{ W m}^{-2} \text{ nm}^{-1}$. However, Zhang et al. (2012) use a different vertical distribution of gases and cloud model, and given the differences in the model representation, this is considered a good agreement. To validate our modelling approach, we modified our model input parameters to match those used by Zhang et al. (2012) to perform a comparison, by using the pressure profiles, aerosol optical properties and UV absorber properties from Crisp (1986), and the SO_2 distribution from Zhang et al. (2012). We then compared the spectra from this modified version of our model to the spectra provided in Zhang et al. (2012) at altitudes of 58, 70 and 112

km, with our results showing very good agreement of the spectral shape and intensity. At 300 nm and 58 km altitude the spectra agree to within 8%, providing validation of the approach used here.

At lower altitudes, sharp increases in scattering are encountered in our simulations at the onset of the cloud layer, and radiative transfer results are strongly sensitive to the prescribed cloud structure. Altitude-specific comparisons in this region of the atmosphere should therefore be treated with extreme caution, since large reductions in irradiance can occur over 1–2 km-scales.

Given the discussion on the variability of SO_2 in Section 2.3, reducing the abundance of SO_2 from ~ 100 ppbv to 10 ppbv (i.e. a $\times 10$ reduction as per the SO_2 variability in Marcq et al., 2020) resulted in a 0.4% change in the fluence at 70 km. Taking the more extreme case of an order of magnitude reduction in SO_2 abundance for the entire column, the maximum reduction is still only $\sim 30\%$ at an altitude of 58 km. Thus, the SO_2 variability whilst not critical, should be considered for more specific analyses, and in any subsequent interpretation/application of the results presented in this study. Note that variation in the abundance of OCS also varies by an order of magnitude (see e.g. Krasnopolsky, 2010; Krasnopolsky, 2012; Rimmer et al., 2021) but is not significant here, since the low abundance and relative size of the absorption cross-section mean there is no appreciable contribution above that of SO_2 .

Integrating over wavelengths 180–400 nm for each irradiance spectrum modelled at regular slices through the atmosphere produces an altitude profile of the UV integrated irradiance, as shown in Fig. 10. The total UV integrated irradiance from the unfiltered solar spectrum at high altitudes is 208 W m^{-2} , composed of 6.3% UVC, 15.8% UVB, and 77.9% UVA wavelengths. This UV integrated irradiance rises to a peak of 226 W m^{-2} at 72 km altitude, just above the ceiling of the upper cloud region, due to increased backscattering from the optically thick cloud layer, leading to a local enhancement of irradiance above the top of atmosphere value. By the top of the aerial habitable zone (62 km), atmospheric scattering and absorption has reduced the total UV integrated irradiance to 86 W m^{-2} , composed of 7% UVC, 16.5% UVB and 76% UVA wavelengths. A representative figure for the (clear sky, noon) total UV integrated irradiance incident on the present-day Earth's surface is $\sim 60 \text{ W m}^{-2}$. The same irradiance level is reached at an altitude of around 60 km in the venusian atmosphere. Both UVC and UVB irradiance contributions have dropped to 0 by 54 km altitude, near the middle of the HZ. By the bottom of the habitable zone, a total integrated irradiance of 5.4 W m^{-2} is delivered by the penetration of UVA.

Given the potentially patchy nature of the unknown UV absorber (e.g. Titov et al., 2018), we included an analysis of the resulting total UV

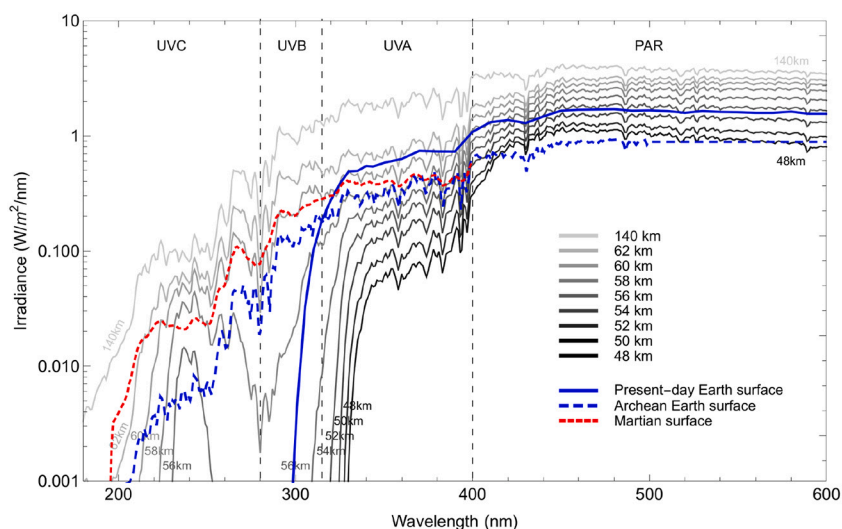


Fig. 9. Irradiance as a function of altitude in the Venus atmosphere, compared to the Archean and present-day Earth conditions (Ranjan and Sasselov, 2017) and present-day Mars (Patel et al., 2004a, 2004b).

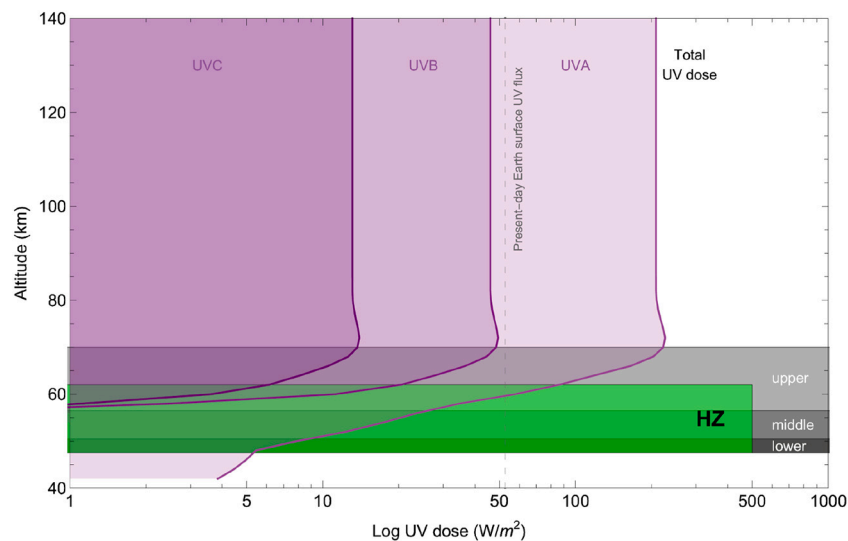


Fig. 10. UV integrated irradiance (200–400 nm) as a function of altitude.

integrated irradiance with and without the unknown UV absorber present. We find the resulting increase in total UV integrated irradiance to be negligible above 80 km, approximately 4% at 70 km, 45% at 64 km and > 100% below 60 km, demonstrating a significant modulation of the UV environment at altitudes <70 km in any such regions with low abundance of the unknown UV absorber. In the case of no unknown UV absorber present, the altitude at which the venusian total UV integrated irradiance becomes comparable to present-day Earth is reached at an altitude of 54 km. Thus, the absence of the unknown UV absorber serves to shift the altitude on Venus where the UV environment is similar to present-day Earth downwards by ~6 km.

To put these figures into the context of microbial survival, *Deinococcus radiodurans* is a polyextremophile bacterium that is extremely resistant to UVC radiation, exhibiting a shoulder in its response curve (i. e. maintaining 100% survival) up to around 500 J m^{-2} , and can survive doses as high as 1000 J m^{-2} , provided it has the opportunity to recover and repair photodamage after exposure (Battista, 1997; Slade and Radman, 2011). At 62 km altitude in the venusian atmosphere we calculate the total UVC irradiance to be 6.1 W m^{-2} . Thus, at the top of the thermally-defined habitable zone, *D. radiodurans* would be able to endure approximately 80 s of UVC irradiance before suffering exponential population decline. *D. radiodurans* is exceedingly resistant to ionising- and ultraviolet-radiation, but is mesophilic with respect to its tolerance of temperature and pH extremes. Considering the environmental conditions of the venusian atmosphere, a more pertinent comparison would be with known microbes resistant to high temperature and acidity. Beblo et al. (2011) tested thermophilic bacteria and hyperthermophilic archaea for survival of UV exposure under anoxic irradiation conditions in liquid suspension. They found that the hyperthermophilic anaerobic archaeon *Archaeoglobus fulgidus* exhibited 90% survival after UVC (254 nm) doses of only 108 J m^{-2} , a fraction of that of *D. radiodurans*. Some bacteria, such as *Bacillus subtilis*, form dormant spores with protected DNA and very high resistance to UVC, but still show 90% survival after a dose of around 300 J m^{-2} (Setlow, 2001). Thus, while an altitude of 62 km in the venusian atmosphere may represent the upper bound of a potential aerial habitable zone defined by the temperature range for survival, the high UV radiation environment at this altitude is likely to be limiting. A point of note is that terrestrial model organisms (and life in general) have evolved to be optimised for a relatively low UV environment. Thus, the comparison to Archean Earth provides a more relevant context in terms of assessing UV stresses relevant to life.

Also relevant to the issue of UV survival is the total dose, and thus the

duration of the exposure. Terrestrial microbes can shield themselves by excreting extracellular sunscreen pigments like scytonemin or colonising within mineral microhabitats, and are afforded the opportunity to repair photodamage during the dark hours of night-time. The rotational period of Venus is 243 terrestrial days, but the cloud tops are observed to flow at around 100 m s^{-1} : the atmosphere has an extreme super-rotation 60-times faster than the planet's spin (Yamamoto and Takahashi, 2004; Lebonnois et al., 2010). Even so, any microbes in the cloud layer would be exposed to the daytime incident UV radiation for at least 48 h at a time.

3.2. Biologically weighted irradiance

The simple integrated UV irradiance, however, neglects the fact that UV wavelengths are not uniformly harmful to microorganisms. The biological effect of DNA damage peaks in the UVC band, as represented in the generalised action spectrum shown in Fig. 8. A suitable metric for assessing the impact of an incident ultraviolet spectrum on microbial survival and habitability is therefore the biologically effective UV irradiance, calculated by the convolution of each irradiance spectrum with the action spectrum as described above.

Fig. 11 shows the Biologically Effective UV irradiance spectra modelled here for the same altitudes as Fig. 9; the top of the atmosphere at 140 km and regular levels through the thermal habitable zone. Our venusian atmosphere modelling results are again compared against those modelled elsewhere for the martian surface (Patel et al., 2004a, 2004b), the present-day Earth's surface and during the ozone-free Archean eon (Ranjan and Sasselov, 2017).

The biologically-weighted UV radiation environment encountered at around 60 km altitude in the venusian atmosphere is similar to that of the surface of the Archean Earth or present-day Mars, dominated by the extremely deleterious flux of energetic UVC and UVB wavelengths. The incident spectrum by 56 km altitude still exhibits a pronounced peak of UVC around 240 nm, but by 54 km altitude the penetration of biologically effective UV radiation is significantly less than that at the present-day terrestrial surface.

Integrating each biologically-weighted spectrum yields the biologically effective UV total irradiance as a function of altitude. Fig. 12 shows this altitude profile, broken down into the contributions from UVC, UVB and UVA wavelength bands. The calculated biologically effective UV total irradiance peaks at 347 W m^{-2} at an altitude of 72 km, declining to 149 W m^{-2} at the top of the habitable zone at 62 km. UVC and UVB wavelengths contribute about three-quarters and one-quarter

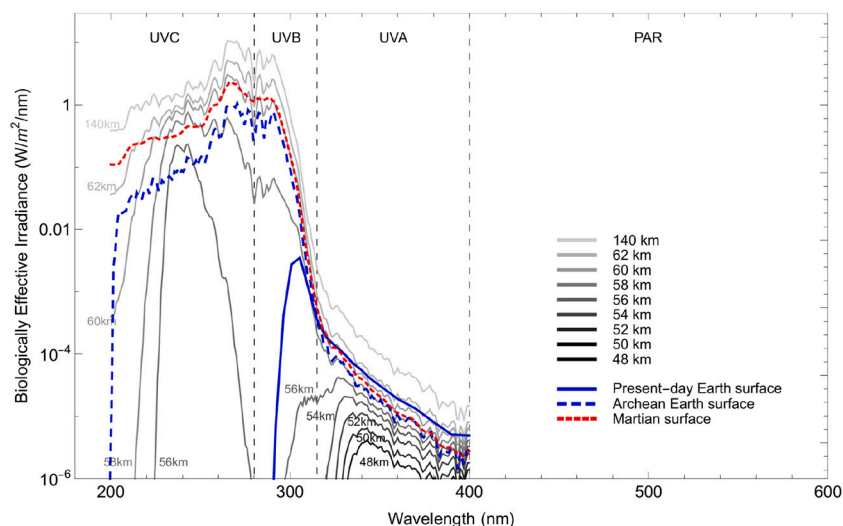


Fig. 11. Biologically effective UV irradiance as a function of altitude in the Venus atmosphere, compared to the Archean and present-day Earth conditions (Ranjan and Sasselov, 2017) and present-day Mars (Patel et al., 2004a, 2004b).

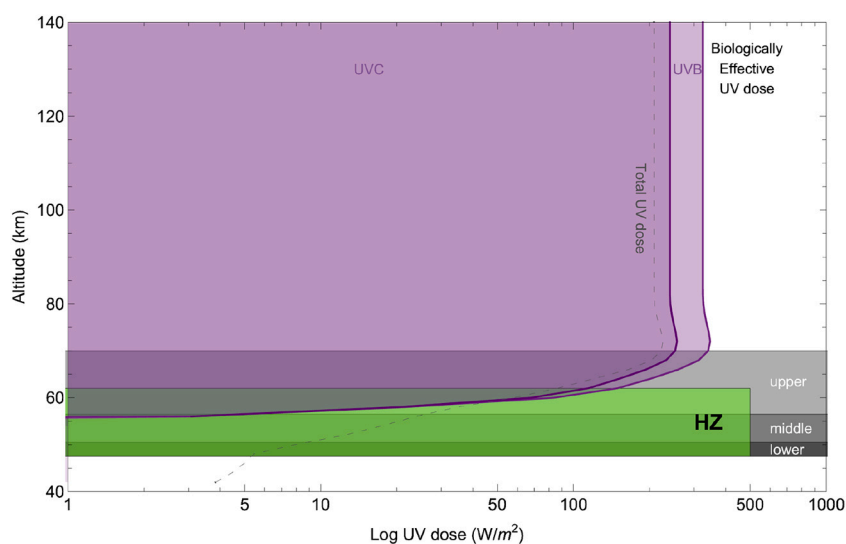


Fig. 12. Biologically effective UV total irradiance (200–400 nm) as a function of altitude.

respectively of the biologically effective UV total irradiance down to the top of the HZ at 62 km altitude. UVC contributes only a tiny amount of this biologically effective UV total irradiance – 0.006–0.005% down to 60 km altitude, after which its proportional contribution increases as shorter wavelengths are completely absorbed.

Using the terrestrial spectra modelled by Ranjan and Sasselov (2017) (convolved with the generalised action spectrum shown in Fig. 8, based on Cockell, 1999) we calculate the biologically effective UV total irradiance on the present-day Earth's surface to be 0.042 W m^{-2} , which agrees well with Cockell and Córdoba-Jabonero (2004) and Cockell and Raven (2004). Similarly, we calculate the biologically effective UV total irradiance incident on the Archean Earth's surface to be 28.9 W m^{-2} . Referring to our modelled altitude profile presented in Fig. 11, this means that the UV radiation environment in the venusian atmosphere becomes less intense than that at the surface of the Archean Earth at altitudes below approximately 59 km. At an altitude of 54 km, the biologically effective UV total irradiance is calculated to be $6.2 \times 10^{-4} \text{ W m}^{-2}$, less than that for the present-day Earth's surface. Thus, by this metric, the lower few kilometres of the venusian atmospheric thermal habitable zone are not challenged by the incident ultraviolet spectrum.

This complements our earlier modelling study that demonstrated the penetration of ionising radiation from cosmic rays is not limiting for life high in the venusian atmosphere (Dartnell et al., 2015). With respect to both ionising cosmic rays and non-ionising solar ultraviolet radiation, the bottom of the potential aerial habitable zone provides an essentially benign radiation environment.

Life on Earth emerged at least 3.5 billion years ago during the Archean era when there was no atmospheric ozone shield (itself a by-product of oxygenic photosynthesis) and high levels of ultraviolet radiation penetrated to the surface. Although some posit that UV may have played a role in driving chemistry leading to the abiogenic synthesis of key organic molecules, or the polymerisation of monomers, on the primordial Earth (e.g. Strigunokova et al., 1986; Powner et al., 2009; Ritson and Sutherland, 2012; Patel et al., 2015; Ranjan and Sasselov, 2017), such short-wavelength, energetic light is in general highly damaging to the complex organic molecules of life and the survival of unprotected cells. Terrestrial microbial life during the Archean may have survived the UV hazard by taking advantage of environmentally-shielded niches, such as beneath minerals or water column, or by synthesising cellular UV-screening compounds. The UV-survival characteristics of microbes

today, adapted to the relatively benign contemporary surface UV environment of Earth, are therefore not necessarily a good guide to the survival of microorganisms in the Archean. It is for this reason that we have compared our modelling results of the venusian ultraviolet radiation environment to that of Archean Earth.

3.3. Photosynthetically active radiation

Alongside the hazard presented by ultraviolet radiation to an aerial biosphere, is the possibility that beneath permanent and dense cloud cover the lower reaches of the habitable zone may not receive sufficient light intensity to support photosynthetic microbial life, which we address briefly here.

Photosynthetically Active Radiation (PAR) is defined as the portion of the spectrum between 400 and 700 nm, over which terrestrial organisms are able to photosynthesise by absorbing light with chlorophyll and accessory pigments such as carotenes and xanthophylls. Previous studies have attempted to quantify the minimum light levels required for supporting photosynthesis. Warren Rhodes et al. (2013) found that hypolithic cyanobacteria communities colonising the underside of translucent quartz rocks in the Namib desert were limited by penetrating light intensity, rather than water availability. The survival threshold was determined to be 0.1% of incident sunlight, which equates to a PAR photon flux of 1–2 $\mu\text{mol}/\text{s}/\text{m}^2$. Meslier et al. (2018) and McKay (2012) infer a similar PAR lower limit for endolithic microbial communities colonising within gypsum crusts in the Atacama desert and within Antarctic sandstones, respectively. Littler et al. (1986) discovered red macroalgae surviving 260 m deep in the oceanic water column on seamounts receiving a sunlight intensity of less than 0.01 $\mu\text{mol}/\text{s}/\text{m}^2$, and in reviewing deep marine photoautotrophs Raven et al. (2000) conclude that 0.01 $\mu\text{mol}/\text{s}/\text{m}^2$ is the lowest photon flux density that oxygenic photosynthesis can operate with, and 0.004 $\mu\text{mol}/\text{s}/\text{m}^2$ is the limit for non-oxygen producing photosynthesis.

Integrating (over 400–700 nm) our modelled spectra of sunlight penetrating the venusian atmosphere down to 42 km altitude, we find that the PAR photon flux is not reduced to less than 1000 $\mu\text{mol}/\text{s}/\text{m}^2$. Such a high PAR photon flux would imply that the visible light intensity is not a limiting factor on photosynthetic organisms in the aerial habitable zone. However, the PAR thresholds summarised above are for the survival of photoautotrophs in the benign environment of the deep-

sea, or protected microniches in the desert. Survival under extreme conditions is determined by a microorganism's energetic balance between photosynthetic energy harvesting and metabolic expenditure on cellular maintenance. Any venusian polyextremophile microbes enduring the combined environmental hazards of high temperature and extremely low pH, alongside UV flux, would be expected to have much higher metabolic energy demands for cell maintenance such as running proton pumps to keep cytosolic acidity nearer neutrality, enzymatic DNA repair and protein turnover (or that of the venusian biochemical analogues).

A more appropriate aspect for survival of the incident radiation in the venusian cloud decks, therefore, is the flux of short wavelengths of UV that cause cellular damage relative to longer-wavelengths of light that can be exploited by photosynthesis to provide energy. By analogy, the euphotic zone (the range of depths supporting photosynthetic organisms) in the water column of Earth's oceans is affected by the relative penetration of UV radiation and attenuation of PAR at greater depths and varies with changes in water turbidity (Kuwahara et al., 2000). We address this vital balance between the energetic expenses of repairing cellular damage and the potential energetic income from photosynthesis by employing the ratio between UV and PAR wavelengths through the atmosphere.

Fig. 13 shows the altitude profile of our modelled biologically effective UV total irradiance (200–400 nm) with that of PAR wavelengths (400–700 nm), as well as the ratio between the two. At the top of the venusian atmosphere, the Biologically Effective UV total irradiance is about one-third that of PAR wavelengths, but Fig. 13 shows that this ratio rapidly declines through the cloud layer of Venus. Ultraviolet radiation, and in particular the most damaging UVC wavelengths, are rapidly absorbed, whilst the atmosphere is less opaque to visible wavelengths which can penetrate more deeply. By the top of the aerial habitable zone (62 km altitude), this weighted UV:PAR ratio has fallen to 0.174, and at the base of the lower cloud level (48 km) the ratio is 5×10^{-7} – ultraviolet radiation makes up only a tiny contribution of the sunlight filtering this far through the clouds. Fig. 13 shows that the weighted UV:PAR ratio drops below that calculated for the surface of the Archean Earth at an altitude of 60 km, and is less than that of the present-day terrestrial surface at an altitude of 54 km.

By this first-order energy balance analysis, therefore, the bottom 6 km of the thermal habitable zone (48–54 km altitude range) offers a

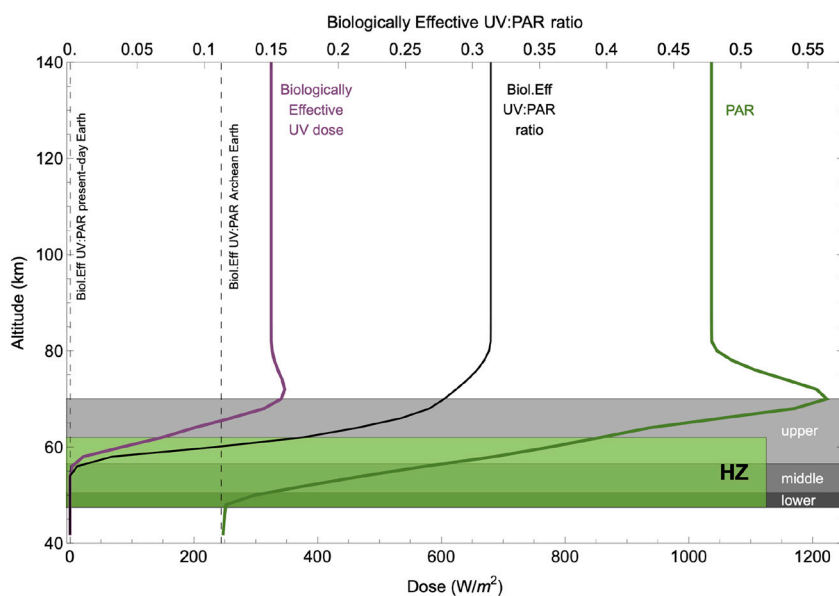


Fig. 13. Photosynthetically Active Radiation (PAR) total irradiance as a function of altitude. Also shown is the biologically effective UV total irradiance (200–400 nm) and the ratio of these two parameters as a function of altitude. For reference, the ratios calculated for the Archean and present-day Earth surface are shown as dashed lines.

radiation environment, in terms of the balance between potentially harmful UV radiation and photosynthetically active radiation, at least as benign as the present-day Earth's surface. This is a conservative estimate, however, and higher altitudes could also be tolerable if venusian microbes incorporate effective ultraviolet screening compounds, or perhaps are even able to photosynthesise with UV wavelengths (Schulze-Makuch et al., 2004).

4. Conclusions

We have modelled the penetration of solar ultraviolet and visible light through the venusian atmosphere to assess the habitability of the cloud layer. Based on thermal considerations alone, a potential aerial habitable zone can be defined across the altitude range set by the lower thermal limit for cell growth of $-20\text{ }^{\circ}\text{C}$ at 62 km and the base of the lower cloud region at 48 km ($100\text{ }^{\circ}\text{C}$), below which liquid droplets have evaporated.

We find that the integrated UV irradiance in the venusian atmosphere rises to a peak of 226 W m^{-2} at 72 km altitude, just above the top of the upper cloud region due to backscattering, but by the top of the aerial habitable zone at 62 km atmospheric scattering and absorption has reduced the UV irradiance to 86 W m^{-2} . The terrestrial UV-resistant extremophile *Deinococcus radiodurans* would only be able to endure 80 s of the UVC irradiance at this altitude before suffering exponential population decline, and so the upper reaches of the thermally-defined aerial habitable zone are severely challenged by the UV penetration. Calculating the biologically-weighted UV irradiance we find that the UV radiation environment of the venusian atmosphere is less intense than that modelled for the surface of the Archean Earth by an altitude of around 59 km, and by around 54 km it is less severe than that of the present-day Earth's surface. Furthermore, the penetration of PAR remains at a terrestrially comparable level throughout the thick cloud layer, which would allow aerial microbes to photosynthesise whilst being screened from harmful UV wavelengths. Based on consideration of thermal conditions, ionising radiation and the UV flux environment of the venusian cloud deck, we define a potential habitable zone that extends from 59 km to 48 km.

This study, and that of the companion paper considering the propagation of solar and galactic cosmic rays (Dartnell et al., 2015), together provide a framework for assessing the potential habitability of the venusian clouds in the context of both ionising and non-ionising radiation. We conclude that the lower few kilometres of the venusian atmospheric habitable zone are not challenged by the incident ultraviolet spectrum or penetrating cosmic rays. We have not considered here the combinatorial effects of other environmental hazards such as acidity and temperature on organism survival but note that active cellular mechanisms for surviving highly acidic environments are energetically expensive and that photosynthesis would offer a reliable energy source.

Whilst this work does not intend to define the feasibility of an aerial habitable zone in general, it does serve to constrain the potential for such a zone from a radiation perspective, demonstrating that a habitable zone is possible from both ionising and non-ionising radiation perspectives, coincident with temperature and pressure conditions that are conducive to the persistence of life. This zone should form the focus of future measurements and analyses by remote and in situ missions to Venus seeking potential microbial life.

Data availability

Datasets related to this article can be found at <https://doi.org/10.21954/ou.rd.c.5277149> with Open Research Data Online (ORDO), an open-source online data repository hosted at the Open University, U.K.

Declaration of Competing Interest

None.

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References

- ASTM E490-00a, 2014. Standard Solar Constant and Zero Air Mass Solar Spectral Irradiance Tables. ASTM International, West Conshohocken, PA, p. 2014. www.astm.org.
- Baker-Austin, C., Dopson, M., 2007. Life in acid: pH homeostasis in acidophiles. *Trends Microbiol.* 15, 165–171.
- Balskus, E.P., Walsh, C.T., 2010. The genetic and molecular basis for sunscreen biosynthesis in cyanobacteria. *Science* 329, 1653–1656.
- Barabash, S., Fedorov, A., Sauvaud, J., Lundin, R., Russell, C., Futaana, Y., et al., 2007. The loss of ions from Venus through the plasma wake. *Nature* 450, 650–653.
- Battista, J., 1997. Against all odds: the survival strategies of *Deinococcus radiodurans*. *Annu. Rev. Microbiol.* 51, 203–224.
- Beblo, K., Douki, T., Schmalz, G., Rachel, R., Wirth, R., Huber, H., et al., 2011. Survival of thermophilic and hyperthermophilic microorganisms after exposure to UV-C, ionizing radiation and desiccation. *Arch. Microbiol.* 193, 797–809.
- Belyaev, D.A., Montmessin, F., Bertaux, J.L., Mahieux, A., Fedorova, A.A., Korablev, O.I., Marq, E., Yung, Y.L., Zhang, X., 2012. Vertical profiling of SO₂ and SO above Venus' clouds by SPICAV/SOIR solar occultations. *Icarus* 217 (2), 740–751.
- Bethmann, B., Schönknecht, G., 2009. pH regulation in an acidophilic green alga - a quantitative analysis. *New Phytol.* 183, 327–339.
- Bézar, B., De Bergh, C., Crisp, D., Maillard, J.P., 1990. The deep atmosphere of Venus revealed by high-resolution nightside spectra. *Nature* 345 (6275), 508.
- Booth, C.R., Morrow, J.H., 1997. The penetration of UV into natural waters. *Photochem. Photobiol.* 65, 254–257.
- Castenholz, R.W., Garcia-Pichel, F., 2012. Cyanobacterial responses to UV radiation. In: Whitton, B.A. (Ed.), *Ecology of Cyanobacteria II: Their Diversity in Space and Time*. Springer, pp. 481–499.
- Cavicchioli, R., 2002. Extremophiles and the search for extraterrestrial life. *Astrobiology* 2, 281–292.
- Chassefière, E., Wieler, R., Marty, B., Leblanc, F., 2012. The evolution of Venus: present state of knowledge and future exploration. *Planet. Space Sci.* 63–64, 15–23.
- Cleaves, H.J., Miller, S.L., 1998. Oceanic protection of prebiotic organic compounds from UV radiation. *Proc. Natl. Acad. Sci. U. S. A.* 95, 7260.
- Cnossen, I., Sanz-Forcada, J., Favata, F., Witasse, O., Zegers, T., Arnold, N.F., 2007. Habitat of early life: solar X-ray and UV radiation at Earth's surface 4–3.5 billion years ago. *J. Geophys. Res.* 112, 611.
- Cockell, C.S., 1998. Ultraviolet radiation, evolution and the pi-electron system. *Biol. J. Linn. Soc.* 63 (3), 449–457.
- Cockell, C., 1999. Life on Venus. *Planet. Space Sci.* 47, 1487–1501.
- Cockell, C.S., 2000. The ultraviolet history of the terrestrial planets - implications for biological evolution. *Planet. Space Sci.* 48, 203–214.
- Cockell, C., Knowland, J., 1999. Ultraviolet radiation screening compounds. *Biol. Rev.* 74, 311–345.
- Cockell, C., Raven, J., 2004. Zones of photosynthetic potential on Mars and the early Earth. *Icarus* 169, 300.
- Cockell, C.S., Catling, D., Davis, W.L., Snook, K., Kepner, R., Lee, P., McKay, C., 2000. The ultraviolet environment of Mars: biological implications past, present, and future. *Icarus* 146, 343–359.
- Cockell, C.S., Cordoba-Jabonero, C., 2004. Coupling of climate change and biotic UV exposure through changing snow-ice covers in terrestrial habitats. *Photochem. Photobiol.* 79 (1), 26–31.
- Cockell, C.S., Higgins, P.M., Johnstone, A.A., 2021. Biologically available chemical energy in the temperate but uninhabitable Venusian cloud layer: what do we want to know? *Astrobiology*. <https://doi.org/10.1089/ast.2020.2280>.
- Connes, P., Connes, J., Benedict, W.S., Kaplan, L.D., 1967. Traces of HCl and HF in the atmosphere of Venus. *Astrophys. J.* 147, 1230–1237.
- Cordoba-Jabonero, C., Zorzano, M., Selsis, F., Patel, M., Cockell, C., 2005. Radiative habitable zones in martian polar environments. *Icarus* 175, 360–371.
- Crisp, D., 1986. Radiative forcing of the Venus mesosphere: I. Solar fluxes and heating rates. *Icarus* 67 (3), 484–514.
- Dartnell, L.R., Nordheim, T.A., Patel, M.R., Mason, J.P., Coates, A.J., Jones, G.H., 2015. Constraints on a potential aerial biosphere on Venus: I. Cosmic rays. *Icarus* 257, 396–405.
- Dillon, J.G., Tatsumi, C.M., Tandingan, P.G., Castenholz, R.W., 2002. Effect of environmental factors on the synthesis of scytonemin, a UV-screening pigment, in a cyanobacterium (*Chroococcidiopsis* sp.). *Arch. Microbiol.* 177, 322–331.
- Donahue, T.M., Hodges, R.R., 1992. Past and present water budget of Venus. *J. Geophys. Res. Space Physics* 97, 6083–6091.
- Driscoll, P., Bercovici, D., 2013. Divergent evolution of Earth and Venus: influence of degassing, tectonics, and magnetic fields. *Icarus* 226, 1447–1464.

- Dubinina, E., Fraenz, M., Fedorov, A., et al., 2011. Ion energization and escape on Mars and Venus. *Space Sci. Rev.* 162, 173–211. <https://doi.org/10.1007/s11214-011-9831-7>.
- Ehling-Schulz, M., Scherer, S., 1999. UV protection in cyanobacteria. *Eur. J. Phycol.* 34, 329–338.
- Ekonomov, A.P., Moshkin, B.E., Moroz, V.I., Golovin, I.M., Gnedykh, V.I., Grigorev, A.V., 1983. The UV-photometry experiment on the Venera-13 and Venera-14 descent modules. *Kosmicheskie Issledovaniia* 21, 254–268.
- Encrenaz, T., Greathouse, T.K., Marcq, E., Sagawa, H., Widemann, T., Bézard, B., Fouchet, T., Lefèvre, F., Lebonnois, S., Atreya, S.K., Lee, Y.J., 2019. HDO and SO₂ thermal mapping on Venus-IV. Statistical analysis of the SO₂ plumes. *Astron. Astrophys.* 623, A70.
- Evdokimova, D., Belyaev, D., Montmessin, F., Korablev, O., Bertaux, J.L., Verdier, L., Lefèvre, F., Marcq, E., 2021. The spatial and temporal distribution of nighttime ozone and sulfur dioxide in the Venus mesosphere as deduced from SPICAV UV stellar occultations. *J. Geophys. Res.* 126 (3) (p.e2020JE006625).
- Frandsen, B.N., Wennberg, P.O., Kjaergaard, H.G., 2016. Identification of OSSO as a near-UV absorber in the Venusian atmosphere. *Geophys. Res. Lett.* 43, 11,146–11,155. <https://doi.org/10.1002/2016GL070916>.
- Friedmann, E.I., 1986. The antarctic cold desert and the search for traces of life on Mars. *Adv. Space Res.* 6, 265–268.
- Greaves, J.S., Richards, A.M., Bains, W., Rimmer, P.B., Sagawa, H., Clements, D.L., et al., 2020. Phosphine gas in the cloud decks of Venus. *Nat. Astron.* <https://doi.org/10.1038/s41550-020-1174-4>.
- Greaves, J.S., Bains, W., Petkowski, J.J., Seager, S., Sousa-Silva, C., Ranjan, S., et al., 2020b. On the Robustness of Phosphine Signatures in Venus' Clouds. [arxiv.org](https://arxiv.org/abs/2020.08.01).
- Greaves, J.S., Richards, A.M., Bains, W., Rimmer, P.B., Clements, D.L., Seager, S., et al., 2020c. Re-analysis of phosphine in Venus' clouds. [arxiv.org](https://arxiv.org/abs/2020.08.01) (astro-ph.EP).
- Greaves, J.S., Richards, A.M.S., Bains, W., et al., 2021. Reply to: no evidence of phosphine in the atmosphere of Venus from independent analyses. *Nat. Astron.* 5, 636–639. <https://doi.org/10.1038/s41550-021-01424-x>.
- Green, A.E., Miller, J.H., 1975. Measures of biologically effective radiation in the 280–340 nm region. *CIAP Monogr.* 5, 2–60.
- Grinspoon, D.H., 1997. *Venus Revealed: A New Look Below the Clouds of Our Mysterious Twin Planet*. Perseus Publishing, Cambridge, MA.
- Grinspoon, D.H., Bullock, M.A., 2003. Did Venus experience one great transition or two? *Bull. Am. Astron. Soc.* 35, 1007.
- Grinspoon, D.H., Bullock, M.A., 2007. *Astrobiology and Venus exploration. In: Exploring Venus as a Terrestrial Planet*, Geophysical Monograph Series, pp. 176–191.
- Hallsworth, J.E., Koop, T., Dallas, T.D., et al., 2021. Water activity in Venus's uninhabitable clouds and other planetary atmospheres. *Nat. Astron.* 5, 665–675. <https://doi.org/10.1038/s41550-021-01391-3>.
- Haus, R., Kappel, D., Arnold, G., 2013. Self-consistent retrieval of temperature profiles and cloud structure in the northern hemisphere of Venus using VIRTIS/VEX and PMV/VENERA-15 radiation measurements. *Planet. Space Sci.* 89, 77–101. <https://doi.org/10.1016/j.pss.2013.09.020>.
- Haus, R., Kappel, D., Arnold, G., 2015. Radiative heating and cooling in the middle and lower atmosphere of Venus and responses to atmospheric and spectroscopic parameter variations. *Planet. Space Sci.* 117, 262–294.
- Herbst, K., Banjac, S., Atri, D., Nordheim, T.A., 2019. Revisiting the cosmic-ray induced Venusian radiation dose in the context of habitability. *A&A* 633, A15.
- Horneck, G., 1993. Responses of *Bacillus subtilis* spores to space environment: results from experiments in space. In: *Origins of Life and Evolution of the Biosphere (Historical Archive)*, 23, p. 37.
- Horneck, G., 1995. Quantification of the biological effectiveness of environmental UV radiation. *J. Photochem. Photobiol. B Biol.* 31, 43–49.
- Kasting, J., 1988. Runaway and moist greenhouse atmospheres and the evolution of Earth and Venus. *Icarus* 74, 472–494.
- Keating, G.M., Bertaux, J.L., Bougher, S.W., Dickinson, R.E., Cravens, T.E., Nagy, A.F., et al., 1985. Models of Venus neutral upper atmosphere: structure and composition. *Adv. Space Res.* 5, 117–171.
- Kliore, A.J., Moroz, V.I., Keating, G.M., 1985. Preface. *Adv. Space Res.* 5, 1–2.
- Krasnopolsky, V.A., 2006. Chemical composition of Venus atmosphere and clouds: some unsolved problems. *Planet. Space Sci.* 54 (13–14), 1352–1359.
- Krasnopolsky, V.A., 2010. Spatially-resolved high-resolution spectroscopy of Venus 2. Variations of HDO, OCS, and SO₂ at the cloud tops. *Icarus* 209 (2), 314–322.
- Krasnopolsky, V.A., 2012. A photochemical model for the Venus atmosphere at 47–112 km. *Icarus* 218 (1), 230–246.
- Krasnopolsky, V.A., 2017. On the iron chloride aerosol in the clouds of Venus. *Icarus* 286, 134–137.
- Kulikov, Y., Lammer, H., Lichtenegger, H.I., Terada, N., Ribas, I., Kolb, C., et al., 2006. Atmospheric and water loss from early Venus. *Planet. Space Sci.* 54, 1425–1444.
- Kuwahara, V.S., Toda, T., Hamasaki, K., Kikuchi, T., Taguchi, S., 2000. Variability in the relative penetration of ultraviolet radiation to photosynthetically available radiation in temperate coastal waters, Japan. *J. Oceanogr.* 56, 399–408.
- Lebonnois, S., Hourdin, F., Eymet, V., Cressin, A., Fournier, R., Forget, F., 2010. Superrotation of Venus' atmosphere analyzed with a full general circulation model. *J. Geophys. Res. Space Physics* 115, 484.
- Limaye, S.S., Mogul, R., Smith, D.J., Ansari, A.H., Stowik, G.P., Vaishampayan, P., 2018. Venus' spectral signatures and the potential for life in the clouds. *Astrobiology* 18, 1181–1198.
- Limaye, S.S., Mogul, R., Baines, K.H., Bullock, M.A., Cockell, C.S., Cutts, J.A., Gentry, D. M., Grinspoon, D.H., Head, J.W., Jessup, K.-L., Kompanichenko, V., Lee, Y.J., Mathies, R., Milojevic, T., Pertzborn, R., Rothschild, L., Sasaki, S., Schulze-Makuch, D., Smith, D.J., Way, M.J., 2021. Venus, an astrobiology target. *Astrobiology*. <https://doi.org/10.1089/ast.2020.2268> ahead of print.
- Lincowski, A.P., Meadows, V.S., Crisp, D., Akins, A.B., Schweiterman, E.W., Arney, G.N., Wong, M.L., Steffes, P.G., Parenteau, M.N., Domagal-Goldman, S., 2021. Claimed detection of PH₃ in the clouds of Venus is consistent with mesospheric SO₂. *Astrophys. J. Lett.* 908 (2), L44. <https://doi.org/10.3847/2041-8213/abde47>.
- Littler, M.M., Littler, D.S., Blair, S.M., Norris, J.N., 1986. Deep-water plant communities from an uncharted seamount off San Salvador Island, Bahamas: distribution, abundance, and primary productivity. *Deep Sea Res. A* 33, 881–892.
- Marcq, E., Jessup, K.L., Baggio, L., Encrenaz, T., Lee, Y.J., Montmessin, F., Belyaev, D., Korablev, O., Bertaux, J.L., 2020. Climatology of SO₂ and UV absorber at Venus' cloud top from SPICAV-UV nadir dataset. *Icarus* 335, 113368.
- McKay, C.P., 2012. Full solar spectrum measurements of absorption of light in a sample of the Beacon Sandstone containing the Antarctic cryptoendolithic microbial community. *Antarct. Sci.* 24, 243–248.
- Melosh, H.J., 1988. The rocky road to panspermia. *Nature* 332, 687–688. <https://doi.org/10.1038/332687a0>.
- Meslier, V., Casero, M.C., Dailey, M., Wierzbos, J., Ascaso, C., Artieda, O., et al., 2018. Fundamental drivers for endolithic microbial community assemblies in the hyperarid Atacama Desert. *Environ. Microbiol.* 20, 1765–1781.
- Messierli, M.A., Amaral-Zettler, L.A., Zettler, E., Jung, S.-K., Smith, P.J., Sogin, M.L., 2005. Life at acidic pH imposes an increased energetic cost for a eukaryotic acidophile. *J. Exp. Biol.* 208, 2569–2579.
- Mogul, R., Limaye, S.S., Way, M.J., Cordova, J.A., 2020. Is Phosphine in the Mass Spectra From Venus' Clouds? [arxiv.org](https://arxiv.org/abs/2020.08.01) (astro-ph.EP).
- Morowitz, H., Sagan, C., 1967. Life in the clouds of Venus? *Nature* 215, 1259–1260.
- Moroz, V.I., Ekonomov, A.P., Golovin, Y.M., Moshkin, B.E., San'ko, N.F., 1983. Solar radiation scattered in the Venus atmosphere: the Venera 11, 12 data. *Icarus* 53 (3), 509–537.
- O'Malley-James, J.T., Kaltenecker, L., 2019. Lessons from early Earth: UV surface radiation should not limit the habitability of active M star systems. *Mon. Not. R. Astron. Soc.* 485, 5598–5603.
- Palmer, K., Williams, D., 1975. Optical constants of sulfuric acid; application to the clouds of Venus? *Appl. Opt.* 14 (1), 208–219.
- Patel, M.R., Zarnecki, J.C., Catling, D.C., 2002. Ultraviolet radiation on the surface of Mars and the Beagle 2 UV sensor. *Planet. Space Sci.* 50 (9), 915–927.
- Patel, M., Bérces, A., Kerékgyártó, T., Rontó, G., Lammer, H., Zarnecki, J., 2004a. Annual solar UV exposure and biological effective dose rates on the Martian surface. *Adv. Space Res.* 33, 1247–1252.
- Patel, M.R., Christou, A.A., Cockell, C.S., Ringrose, T.J., Zarnecki, J.C., 2004b. The UV environment of the Beagle 2 landing site: detailed investigations and detection of atmospheric state. *Icarus* 168 (1), 93–115.
- Patel, B.H., Percivalle, C., Ritson, D.J., Duffy, C.D., Sutherland, J.D., 2015. Common origins of RNA, protein and lipid precursors in a cyanosulfidic protometabolism. *Nat. Chem.* 7, 301–307. <https://doi.org/10.1038/NCHEM.2202>.
- Persson, M., Futaana, Y., Ramstad, R., Masunaga, K., Nilsson, H., Hamrin, M., et al., 2020. The Venusian atmospheric oxygen ion escape: extrapolation to the early solar system. *J. Geophys. Res. Space Physics* 125, 385.
- Pollack, J.B., Toon, O.B., Whitten, R.C., Boese, R., Ragent, B., Tomasko, M., Esposito, L., Travis, L., Wiedman, D., 1980. Distribution and source of the UV absorption in Venus' atmosphere. *J. Geophys. Res. Space Physics* 85 (A13), 8141–8150.
- Pollack, J.B., Dalton, J.B., Grinspoon, D., Wattson, R.B., Freedman, R., Crisp, D., Allen, D. A., Bézard, B., DeBergh, C., Giver, L.P., Ma, Q., 1993. Near-infrared light from Venus' nightside: a spectroscopic analysis. *Icarus* 103 (1), 1–42.
- Powner, M., Gerland, B., Sutherland, J., 2009. Synthesis of activated pyrimidine ribonucleotides in prebiotically plausible conditions. *Nature* 459, 239–242. <https://doi.org/10.1038/nature08013>.
- Ranjan, S., Sasselov, D.D., 2017. Constraints on the early terrestrial surface UV environment relevant to prebiotic chemistry. *Astrobiology* 17, 169–204.
- Ranjan, S., Wordsworth, R., Sasselov, D.D., 2017a. Atmospheric constraints on the surface UV environment of Mars at 3.9 Ga relevant to prebiotic chemistry. *Astrobiology* 17, 687–708.
- Ranjan, S., Wordsworth, R., Sasselov, D.D., 2017b. The surface UV environment on planets orbiting M dwarfs: implications for prebiotic chemistry and the need for experimental follow-up. *Astrophys. J.* 843, 110.
- Raven, J.A., Kübler, J.E., Beardall, J., 2000. Put out the light, and then put out the light. *J. Mar. Biol. Assoc. U. K.* 80, 1–25.
- Rimmer, P.B., Jordan, S., Constantinou, T., Woitke, P., Shorttle, O., Hobbs, R., Paschodimas, A., 2021. Hydroxide salts in the clouds of Venus: their effect on the sulfur cycle and cloud droplet pH. *Planet. Sci. J.* 2 (4), 133.
- Ritson, D., Sutherland, J.D., 2012. Prebiotic synthesis of simple sugars by photoredox systems chemistry. *Nat. Chem.* 4 (11), 895–899. <https://doi.org/10.1038/nchem.1467>.
- Rontó, G., Bérces, A., Lammer, H., Cockell, C., Molina-Cuberos, G., Patel, M., Selsis, F., 2003. Solar UV irradiation conditions on the surface of Mars. *Photochem. Photobiol.* 77, 34–40.
- Rosow, W.B., Del Genio, A.D., Limaye, S.S., Travis, L.D., Stone, P.H., 1980. Cloud morphology and motions from Pioneer Venus images. *J. Geophys. Res. Space Physics* 85 (A13), 8107–8128.
- Rugheimer, S., Segura, A., Kaltenecker, L., Sasselov, D., 2015. UV surface environment of earth-like planets orbiting FGKM stars through geological evolution. *Astrophys. J.* 806, 137.
- Sagan, C., 1961. The planet Venus. *Science* 133, 849–858.
- Sandor, B.J., Clancy, R.T., Moriarty-Schieven, G., Mills, F.P., 2010. Sulfur chemistry in the Venus mesosphere from SO₂ and SO microwave spectra. *Icarus* 208 (1), 49–60.
- Sato, S., Cuntz, M., Guerra Olvera, C.M., Jack, D., Schröder, K.P., 2014. Habitability around F-type stars. *Int. J. Astrobiol.* 13, 244–258.

- Schulze-Makuch, D., Irwin, L., 2002. Reassessing the possibility of life on Venus: proposal for an astrobiology mission. *Astrobiology* 2, 197–202.
- Schulze-Makuch, D., Grinspoon, D., Abbas, O., Irwin, L., Bullock, M., 2004. A sulfur-based survival strategy for putative phototrophic life in the Venusian atmosphere. *Astrobiology* 4, 11–18.
- Schulze-Makuch, D., Irwin, L.N., Fairén, A.G., 2013. Drastic environmental change and its effects on a planetary biosphere. *Icarus* 225, 775–780.
- Seager, S., Petkowski, J.J., Gao, P., Bains, W., Bryan, N.C., Ranjan, S., Greaves, J., 2020. The Venusian lower atmosphere haze as a depot for desiccated microbial life: a proposed life cycle for persistence of the Venusian aerial biosphere. *Astrobiology* 21, 1206–1223. <https://doi.org/10.1089/ast.2020.2244>.
- Segura, A., Krellove, K., Kasting, J.F., Sommerlatt, D., Meadows, V., Crisp, D., et al., 2003. Ozone concentrations and ultraviolet fluxes on Earth-like planets around other stars. *Astrobiology* 3, 689–708.
- Seiff, A., Kirk, D.B., Young, R.E., Blanchard, R.C., Findlay, J.T., Kelly, G.M., Sommer, S. C., 1980. Measurements of thermal structure and thermal contrasts in the atmosphere of Venus and related dynamical observations: results from the four Pioneer Venus probes. *J. Geophys. Res. Space Physics* 85 (A13), 7903–7933.
- Seiff, A., Schofield, J.T., Kliore, A.J., Taylor, F.W., Limaye, S.S., Revercomb, H.E., et al., 1985. Models of the structure of the atmosphere of Venus from the surface to 100 kilometers altitude. *Adv. Space Res.* 5, 3–58.
- Setlow, P., 2001. Resistance of spores of *Bacillus* species to ultraviolet light. *Environ. Mol. Mutagen.* 38, 97–104.
- Shao, W.D., Zhang, X., Bierson, C.J., Encrenaz, T., 2020. Revisiting the sulfur-water chemical system in the middle atmosphere of Venus. *J. Geophys. Res.* 125 (8) (p. e2019JE006195).
- Slade, D., Radman, M., 2011. Oxidative stress resistance in *Deinococcus radiodurans*. *Microbiol. Mol. Biol. Rev.* 75, 133–191.
- Strigunkova, T.F., Lavrentiev, G.A., Otroshchenko, V.A., 1986. Abiogenic synthesis of oligonucleotides on kaolinite under the action of ultraviolet radiation. *J. Mol. Evol.* 23, 290–293. <https://doi.org/10.1007/BF02100636>.
- Svedhem, H., Titov, D., Taylor, F., Witasse, O., 2007. Venus as a more Earth-like planet. *Nature* 450, 629–632.
- Taylor, F.W., 2006. Venus before Venus express. *Planet. Space Sci.* 54 (13–14), 1249–1262.
- Thompson, M.A., 2020. The statistical reliability of 267-GHz JCMT observations of Venus: no significant evidence for phosphine absorption. *Mon. Not. R. Astron. Soc. Lett.* 501, L18–L22.
- Titov, D.V., Bullock, M.A., Crisp, D., Renno, N.O., Taylor, F.W., Zasova, L.V., 2007. Radiation in the atmosphere of Venus. In: *Geophysical Monograph-American Geophysical Union*, 176, p. 121.
- Titov, D.V., Ignatiev, N.I., McGouldrick, K., Wilquet, V., Wilson, C.F., 2018. Clouds and hazes of Venus. *Space Sci. Rev.* 214 (8), 1–61.
- Tomasko, M.G., Smith, P.H., Suomi, V.E., Sromovsky, L.A., Revercomb, H.E., Taylor, F. W., Martonchik, D.J., Seiff, A., Boese, R., Pollack, J.B., Ingersoll, A.P., 1980. The thermal balance of Venus in light of the Pioneer Venus mission. *J. Geophys. Res. Space Physics* 85 (A13), 8187–8199.
- Tomasko, M.G., Doose, L.R., Smith, P.H., 1985. The absorption of solar energy and the heating rate in the atmosphere of Venus. *Adv. Space Res.* 5 (9), 71–79.
- Toon, O.B., Turco, R.P., Pollack, J.B., 1982. The ultraviolet absorber on Venus: amorphous sulfur. *Icarus* 51 (2), 358–373.
- Tsang, C.C., Irwin, P.G., Wilson, C.F., Taylor, F.W., Lee, C., de Kok, R., Drossart, P., Piccioni, G., Bezard, B., Calcutt, S., 2008. Tropospheric carbon monoxide concentrations and variability on Venus from Venus Express/VIRTIS-M observations. *J. Geophys. Res.* 113 (E5).
- Vandaele, A.C., Korablev, O., Belyaev, D., Chamberlain, S., Evdokimova, D., Encrenaz, T., Esposito, L., Jessup, K.L., Lefèvre, F., Limaye, S., Mahieux, A., 2017a. Sulfur dioxide in the Venus atmosphere: I. Vertical distribution and variability. *Icarus* 295, 16–33.
- Vandaele, A.C., Korablev, O., Belyaev, D., Chamberlain, S., Evdokimova, D., Encrenaz, T., Esposito, L., Jessup, K.L., Lefèvre, F., Limaye, S., Mahieux, A., 2017b. Sulfur dioxide in the Venus atmosphere: II. Spatial and temporal variability. *Icarus* 295, 1–15.
- Villanueva, G.L., Cordiner, M., Irwin, P.G.J., et al., 2021. No evidence of phosphine in the atmosphere of Venus from independent analyses. *Nat. Astron.* 5, 631–635. <https://doi.org/10.1038/s41550-021-01422-z>.
- Walker, J., 1975. Evolution of the atmosphere of Venus. *J. Atmos. Sci.* 32, 1248–1256.
- Warren Rhodes, K.A., McKay, C.P., Boyle, L.N., Wing, M.R., Kiekebusch, E.M., Cowan, D. A., Rhodes, K.L., 2013. Physical ecology of hypolithic communities in the central Namib Desert: the role of fog, rain, rock habitat, and light. *J. Geophys. Res.* 118, 1451–1460.
- Way, M.J., Del Genio, A.D., 2020. Venusian habitable climate scenarios: modeling Venus through time and applications to slowly rotating Venus-like exoplanets. *J. Geophys. Res. Space Physics* 125, 1047.
- Way, M.J., Del Genio, A.D., Kiang, N.Y., Sohl, L.E., Grinspoon, D.H., Aleinov, I., et al., 2016. Was Venus the first habitable world of our solar system? *Geophys. Res. Lett.* 43, 8376–8383.
- Wiscombe, W.J., 1980. Improved Mie scattering algorithms. *Appl. Opt.* 19 (9), 1505–1509.
- Worth, R.J., Sigurdsson, S., House, C.H., 2013. Seeding life on the moons of the outer planets via lithopanspermia. *Astrobiology* 13 (12), 1155–1165. <https://doi.org/10.1089/ast.2013.1028>.
- Yamamoto, M., Takahashi, M., 2004. Dynamics of Venus' superrotation: the eddy momentum transport processes newly found in a GCM. *Geophys. Res. Lett.* 31, L09701. <https://doi.org/10.1029/2004GL019518>.
- Young, A.T., 1974. Venus clouds: structure and composition. *Science* 183 (4123), 407–409. <https://doi.org/10.1126/science.183.4123.407>.
- Zhang, X., Liang, M.C., Montmessin, F., Bertaux, J.L., Parkinson, C., Yung, Y.L., 2010. Photolysis of sulphuric acid as the source of sulphur oxides in the mesosphere of Venus. *Nat. Geosci.* 3 (12), 834.
- Zhang, X., Liang, M.C., Mills, F.P., Belyaev, D.A., Yung, Y.L., 2012. Sulfur chemistry in the middle atmosphere of Venus. *Icarus* 217 (2), 714–739.