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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 do no below the lower thermal limit of cell growth and below which temperatures exceld 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 (100) intensity in the atmosphere. We simulated the penetration of solar unraviolet 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 perial habitable zone (62 km) the incoming solar irradiance creates a severely chalking UV environment, with extremophiles such as Deinococcus radiodurans experted to be able to endure these UV conditions for approximately 80 seconds. A 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. County, longer wavelength photosynthetically active light continues to penatrate 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.

Keywords: Venus, astrobiology, ultraviolet observations

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 vater 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 (Chassefiere et al., 2012), Persson et al (2023) have recently argued from measurements by Venus Express that present-acvescape rates cannot account for the loss of a past Earth-like ocean. However, the possibility remains that the Venus provided an early environment sufficiently rie nent and long-lived (Kasting, 1988; Grinspoon and Bullock, 2003; Way et al., 016; Way and Del Genio, 2020), for life to have originated. Alternatively, such an early habitable surface environment could have been colonized through lithopans, ermia by microbes transferred from Earth by meteorite impacts (e.g. Melosh 1538; 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 'ife in the clouds

Given the present-dal 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).

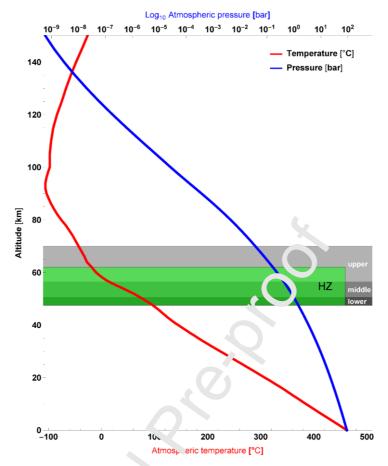
Highly acidic conditions are very damaging to the complex molecules of life, and terrestrial acidophiles employ both passive and active mechanisms to maintain the internal environment of their cytosol at much closer to neutrality, as well as rapidly repairing damage as it occurs. These adaptions include a more impermeable cell membrane, cytosolic buffering molecules, maintaining a reversed membrane potential (i.e. concentrating positive-charged ions inside up 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 unice!!ular green algae *Chlamydomonas sp.* isolated from Rio Tinto acid mine drain ge system was found to consume 7% more ATP per second at pH2 than pH7 ace 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 10% 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 patrients 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 et al., 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 hypera dophiles) cannot survive pH 0 at temperatures higher than 65 °C. Given that any runtive 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 enusian 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. Figure 1 plots the temperature and pressure profiles through the venusian amosphere (data from Venus International Reference Atmosphere: Kliore ct al., 1985; Seiff et al., 1985; Keating et al., 1985), and so shows that these limits wall 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 perign to life. This potential habitable zone is indicated in Figure 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 aerosois 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 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) (Castenholtz 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 vell as the conjugated structures of unsaturated aliphatic molecules like the intry acids and lipids of cell membranes (Cockell, 1999). UVC and UVB radiation transfore results in DNA lesions and protein damage, including photosystems, and is very deleterious to cellular survival. Longer wavelength UVA also inhibits phatos inthesis, 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 an a various free radicals which causes indirect damage to a wide range of a cell's bic olecules (Dillon et al., 2002; Castenholtz and Garcia-Pichel, 2012).

A terrestrial cell exposed to short ravelength UV radiation thus suffers DNA lesions and damage to its proteins and photosystem (if present), which are extremely deleterious to survival. Eve. if life on Venus (or elsewhere) were not based on precisely the same biomorpules as terrestrial biology – DNA/RNA, proteins, lipid bilayers – it can be presumed to require complex organic chemistry, including many biomolecular moietics 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. Provious 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 an ituaes is comparable to that on the surface of archean Earth when photosynthetic in the 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).

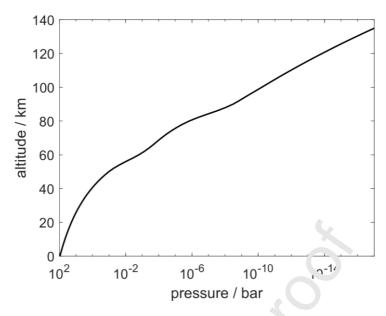
Previous studies have considered to impact of stellar UV radiation on potentially habitable bodies in the context of astrobiology. These include modelling the UV spectrum on the surface of Mars under both current and modelled ancient atmospheric conditions (Cockell et al., 2000; Ronto et al., 2003; Patel et al., 2004a; Patel et al., 2004b; Cordcha-Jabonero et al., 2005; Ranjan et al., 2017); 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; Cnossen 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., 2017; O'Malley-James and Kaltenegger, 2019). Cockell (2000) used a single scattering carbon dioxidenitrogen 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

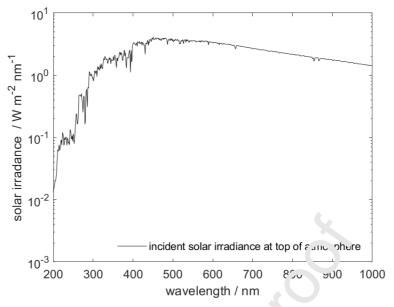
We have utilised a radiative transfer model originally developed for the martian atmosphere (Patel et al., 2002) adapted to the conditions of the Venus atmosphere. Details of the method can be found in Patel et al., (2002) and Patel et al., (2004) and are summarised here for clarity including the adaptations 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 in 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 in colation 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 (se +i.or 2.3). The Rayleigh scattering crosssection is calculated for each species usfining the scattering contribution to the extinction cross section. Laborato v m easurement 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 zer. (in these cases, only the Rayleigh scattering The optical depth contribution is then calculated contributes to extinction). considering the combinatio: of the extinction cross-section and the layer column abundance of each specie. Aerosol scattering is accounted for by considering the Mie scattering from the 'loud particles (mode 1-3 particles) using the optical properties shown in Figure 6 (see section 2.4). We employ a thermal structure for the Venus atmosphere described by Haus et al., (2013a) to determine the pressure (and thus species abondance) in each model layer assuming hydrostatic equilibrium. The resulting pressure profile is shown in Figure 2.



rigure 2. rressure-unnuae projile usea in the radiative model.

2.2 Solar spectrum

We use the ASTM E-490 Air Mass Zero (AMO) Standard Spectra (ASTM E490-00a (2014)) corrected for the Sun-Venur distance as our input solar irradiance, Figure 3 The ASTM E490 AMO solar irradiance is a collation of data from satellites, space shuttle missions, high-altitude circraft, rocket soundings, ground-based solar telescopes, and modelled spect at radiance. The UV (200-400nm) irradiance at the top of the Venus atmosphere is ~200 Wm⁻², which is approximately twice that at Earth and follows the inverce square law for Venus' average distance of 0.72 AU. Half of the UV radiation incident on Venus is absorbed at the cloud tops (~65 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).



rigure 5. Solul illudiance incluent at the top of the venus atmos, here. (ASTIVI E450-000, 2014)

2.3 Atmospheric composition

The atmosphere of Venus comprises pred minately of carbon dioxide (CO₂) with the other major gas being nitrogen (N2) and contains numerous trace gases that include SO₂, SO, HCI, 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 SP'C+ Y-UV occultation observations show two distinct layers of SO₂ in the Venus mesc sphere. 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 later (35-105 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 brown 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 Figure 4 between 0 and 80 km and were taken from Tsang et al. (2008). The SO₂ mixing ratio above 85 km was taken from Figure 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,b, 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 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 CO₂ and N₂ are fractional abundances of 0.965 and 0.035 respectively and

assumed to be vertically uniform. HCI 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; Bezard *et al.*, 1990).

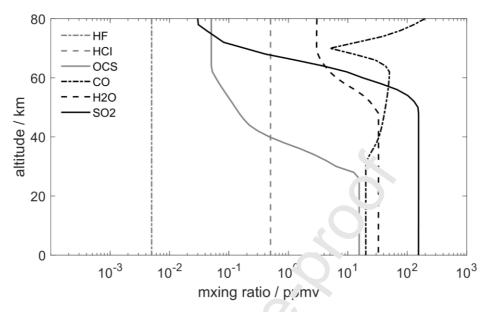
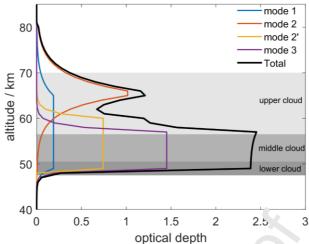


Figure 4: The vertical distribution of the trace gasses in the Venus atmosphere (Tsang et al., 2008).

The Venus atmosphere is dominater by thick aerosol clouds that are made of small droplets of sulfuric acid of concentration 75-90% in H₂O. 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 in in it 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 layer and also in the mesosphere (Crisp, 1986). General agreement between radictive models and the Venera descent probes has been accomplish by describing the clouds using four size ranges, known as 'modes'; mode 1, mode 2, mode 2' and node 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 Figure 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 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.



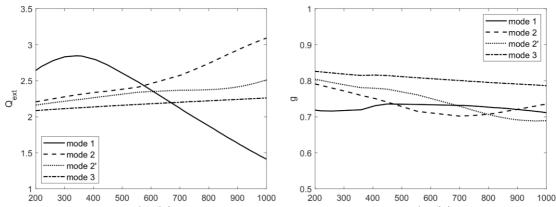
optical depth rigure 3. vertical structure of the venusian π₂304 chouns (παας et al., 2015)

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 depoted (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 H₂SO₄ in H₂O taken from Palmor 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 Figure 6), as well as the single scattering albedo which has a value of unity across the wavelength range considered here.

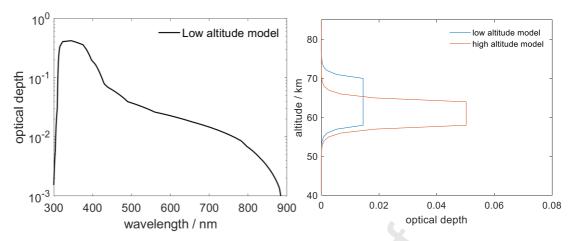
Table 1: Modal radii and a spersion for the aerosol log-normal distributions (Pollack et al., 1993)

Mode	<u>,</u>	1	2	2'	3
Radius	(0.3	1.00	1.40	3.65
Sigma	-	1.56	1.29	1.23	1.28



rigure o. (left) The extinction efficiency of mode 1, mode 2, mode 2 and mode 3 H_2SO_4 derosol 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.

Observations of the venusian atmosphere have netected the presence of an unknown UV absorber at wavelengths shorter than CCC 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 aeroso, has remained elusive and debated for many years. Recent results have proposed canadates for the UV absorber, such as the S₂O₂ isomers, cis-OSSO and trans-DSSO (Frandsen et al., 2016), or FeCl3 (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 actiate 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 65 km (Ekonomov 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 & al., 1980) which shows little to no absorption below 57.5 km; the upper extent of in a 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 crosssection 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 Figure 7, as well as its vertical distribution which was assumed to follow the low altitude model description from Haus et al., (2015).



et al., 2015). (right) The vertical distribution of the unknown UV absorber (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 DN) van age 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 v ave ength. For terrestrial microorganisms, DNA damage and loss of cellular viability is 'he 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 in . "tian studies (e.g. Cockell et al., 2000; Patel et al., 2004; Cordoba-Jabonero et al. 1005). Here, we use the generalised DNA action spectrum shown in Figure 3, aerived 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, 1974). Ideally, a standard action spectrum would be used < 280 nm, but due to the lack of action spectrum data at theses wavelengths, the approach of Cockell (1999) is deemed appropriate for this general analysis of model organism response. A factor ×2 increase in fluence <280 nm results in a factor ×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 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.

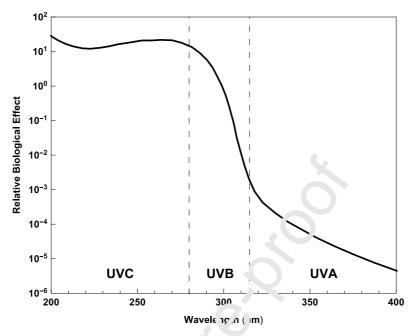


Figure 8: The action spectrum used to calculate his raically effective UV irradiance, based on that for DNA presented in Cockell (1999), normaliser to 3 00 nm.

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

Figure 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., 2004). Figure 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 ~0.1 W m⁻² nm⁻¹, compared to this study with a value of ~0.4 W m⁻² 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 SO₂ 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 intentity. 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 arc 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/s cales.

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.c. a ×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 requirition is still only ~30% at an altitude of 58 km. Thus, the SO_2 variability whist 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. Kranopolsky, 2010; Krasnopolsky, 2012; Rimmer et al., 2021) but is not significant user, since the low abundance and relative size of the absorption cross-section mean there is no appreciable contribution above that of SO_2 .

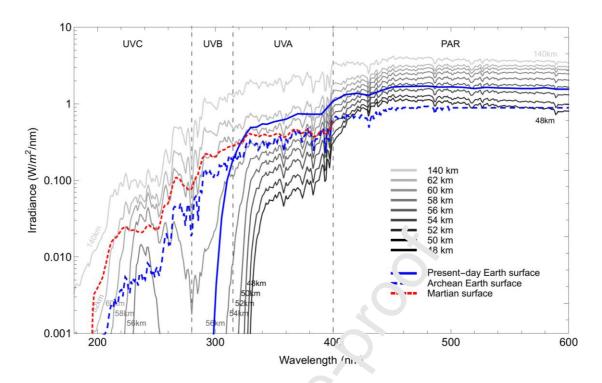


Figure 9: Irradiance as a function of altitude in the Vinu atmosphere, compared to the Archean and present-day Earth conditions (Ranjan and Sasselov, 2017) and present-day Mars (Patel et al., 2004).

Integrating over wavelengths 180-400 im for each irradiance spectrum modelled at regular slices through the atmosphere produces an altitude profile of the UV integrated irradiance, as shown in Figure 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 warelengths. 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 in ad ance above the top of atmosphere value. By the top of the aerial habitable zone (62 km), atmospheric scattering and absorption has reduced the total U' integrated irradiance to 86 W m⁻², composed of 7% UVC, 16.5% UVB and 76% UVA vavelengths. A representative figure for the (clear sky, noon) total UV integrated irradiance incident on the present-day Earth's surface is ~60 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 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.

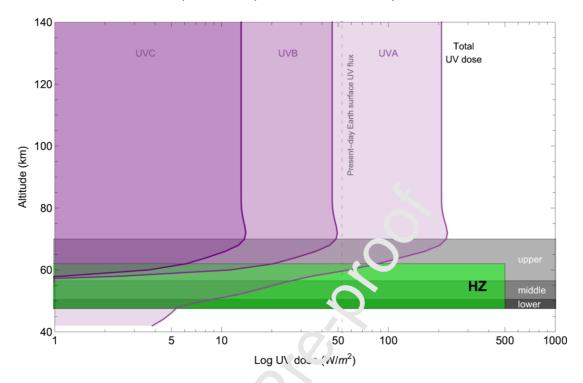


Figure 10: UV integrated irradiance (200-40 / nm as a function of altitude.

To put these figures into the cor. text 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 survice 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 haraciance to be 6.1 W m⁻². Thus, at the top of the thermallydefined habitable zone, D. radiodurans would be able to endure approximately 80 seconds of UVC nraulance before suffering exponential population decline. D. radiodurans is excerdingly 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

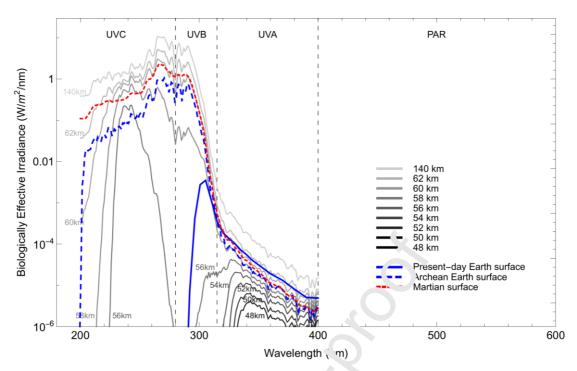
is that terrestrial model organisms (and life in general) have evolved to be optimised for a relatively low UV environment. Thus, the comparison to Archean Earth provides a more relevant context in terms of assessing UV stresses relevant to life.

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 hours at a time.

3.2 Biologically weighted irradiance

The simple integrated UV irradiance, however, neglect the fact that UV wavelengths are not uniformly harmful to microorganisms. The phological effect of DNA damage peaks in the UVC band, as represented in the generalised action spectrum shown in Figure 8. A suitable metric for assessing the in pact 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.

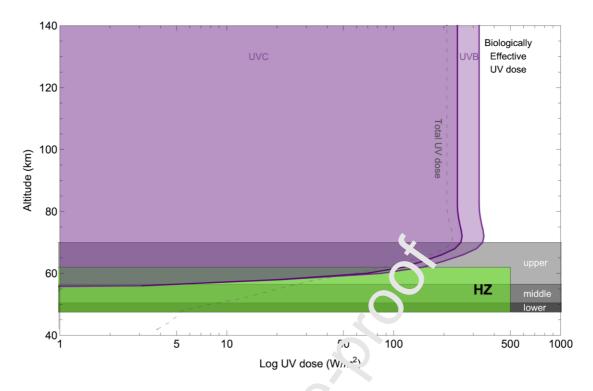
Figure 11 shows the Biologically Effective UV irradiance spectra modelled here for the same altitudes as Figure 9; the top of the atmosphere at 140 km and regular levels through the thermal habitable zone. Our venusian atmosphere modelling results are again compared against those modelled elsewhere for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



compared to the Archean and present-day Earth conditions (Ranjan and Sasselov, 2017) and present-day Mars (Patel et al., 2004).

The biologically-weighted UV radiation and ronment 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 arour d 2-3 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 biologica. V-weighted spectrum yields the biologically effective UV total irradiance as a function of altitude. Figure 12 shows this altitude profile, broken down into the contributions from UVC, UVB and UVA wavelength bands. The calculated biologica. Veffective 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 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 Pan an and Sasselov (2017) (convolved with the generalised action spectrum shown in Figure 8, based on Cockell, 1999) we calculate the biologically effective 'JV .otal irradiance on the present-day Earth's surface to be 0.042 W m⁻², which agress well with Córdoba-Jabonero et al., (2003) and Cockell and Raven (2004). Sincilarly, 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 Figure 11, this means that the UV radiation environment in the venusian atmosphere becomes less intense than that at the surface of the Archan Earth at altitudes below approximately 59 km. At an altitude of 54 km, the biologically effective UV total irradiance is calculated to be 6.2×10^{-4} 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 challen, ed 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. Strigunkova et al., 1986; Powner et al., 2009; Ritson & Sutherland, 2012; Patel et al., 2015; Ranjan & Sasselov, 2016), 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 rocein ne 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 charal hyll and accessory pigments such as carotenes and xanthophylls. Previous tudies have attempted to quantify the minimum light levels required for st.ppt rting photosynthesis. Warren Rhodes et al. (2013) found that hypolithic cyanobacaria 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 µmol/s/m². Meslier et al. (2018) and Mc (ay (2012) infer a similar PAR lower limit for endolithic microbial communities colonising within gypsum crusts in the Atacama desert and within Antarctic sandstonas, respectively. Littler et al. (1986) discovered red macroalgae surviving ?c? m deep in the oceanic water column on seamounts receiving a sunlight intensity of less than 0.01 µmol/s/m², and in reviewing deep marine photoautoticohs Raven et al. (2000) conclude that 0.01 μmol/s/m² is the lowest photon flux density that oxygenic photosynthesis can operate with, and 0.004 μmol/s/m² 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 µmol/s/m². 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.

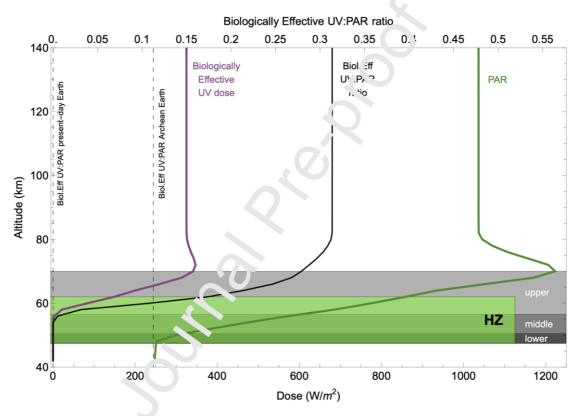


Figure 13: Photosynthetically Active Radiation (PAR) total irradiance as a function of altitude. Also shown is the biologically effective UV total irradiance (200-400 nm) and the ratio of these two parameters as a function of altitude. For reference, the ratios calculated for the Archean and present-day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

Figure 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 Figure 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. Figure 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 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 anne can be defined across the altitude range set by the lower thermal limit for cell growth of -20°C at 62 km and the base of the lower cloud region at 48 km (100°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 Deinc accus radiodurans would only be able to endure 80 seconds 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 severally challenged by the UV penetration. Calculating the biologically-weighted UV radiance we find that the UV radiation environment of the venusian atmospherative 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 pissent-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 the 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.

5 Data availability

Datasets related to this article can be found at http://dx.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.

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Highlights for the manuscript titled "Constraints on a potential aerial biosphere on Venus: II. Ultraviolet radiation" by Patel et al.

- At 54 km altitude on Venus the biologically weighted UV irradiance is less than at Earth's surface
- At 59 km in the venusian atmosphere the biologically weighted UV irradiance is similar to Archean Earth
- The ratio of UV and PAR radiation between 54 48 km is as benign as the present-day Earth's surface
- A potential thermal and radiation habitable zone extends from 59 to 48 km on Venus