Lessons from Earth Aerobiology for Venus Habitability Science

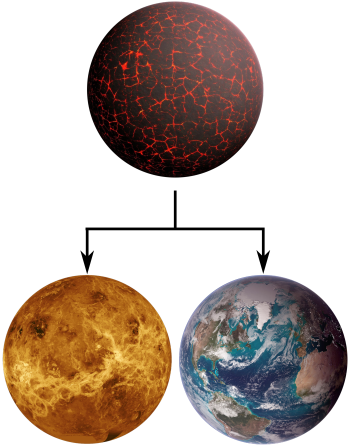
Ames Aerobiology Laboratory (ABL)

D. Gentry (diana.gentry@nasa.gov)[1]

[1]NASA Ames Research Center

Habitability of the Venus Atmosphere
Venus Panel of the NAS Planetary Science and Astrobiology Decadal Survey
19 May 2021

Venus clouds: why the astrobiology interest?



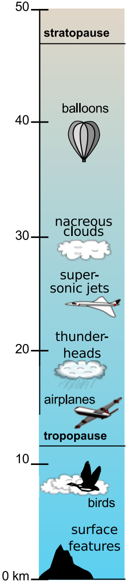
Early history favorable for life?

- Early planetary history believed to be similar to Earth's
  - Surface water (ground water, lakes, or oceans)[1] & geological activity
  - By analogy, potential for an Earth-like biochemistry (water, carbon, etc.)
- Could life have persisted in the remaining water, i.e., in the sulfuric acid cloud layer?

Some currently unexplained observations:

- absorption properties[2]
- phosphine[3]
- sulfur & other chemical cycling[4]

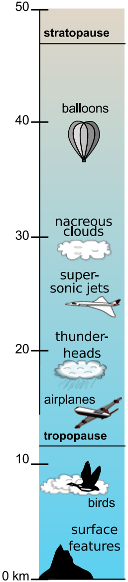
Earth’s atmosphere is full of life (part 1)



The troposphere is clement and cloudy

- 10^4–10^8 $\frac{\text{cell}}{\text{m}^3}$ recovered viable above ground [5]
- 10^1–10^6 $\frac{\text{cell}}{\text{m}^3}$ recovered viable above ocean [6]
- $\sim 25\,\%$ of other particulates are bioaerosols (incl. dead cells, fragments) [7]
- 10^3–10^5 $\frac{\text{cell}}{\text{mL}}$ observed in ground-level cloud water
  - at least some are metabolically active [8–10]
- biodiversity may approach that of soil [11], despite much lower biomass
- viable microbes are transported globally as dust [12]
- many measurable geochemical and physical effects:
  - carbon, nitrogen, and sulfur cycling [13]
  - surface [14] and cloud albedo [15]
  - cloud formation and precipitation [16;17]
  - fog and rain water chemistry [18;19]

Earth's atmosphere is full of life (part 2)

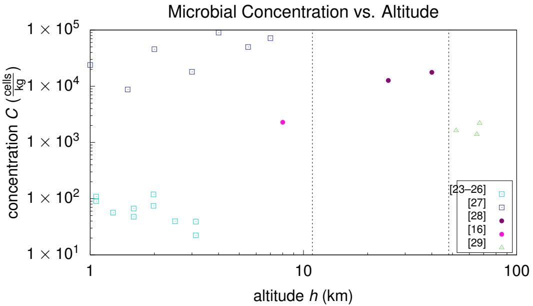


The stratosphere is a better Venus cloud layer analogue

- Relatively isolated from the surface (exceptions: volcanic, extreme weather, anthropogenic)
- Residence time can be weeks to months
- Overall very low water content ($\psi = -1.5 \times 10^9$ Pa)
- Significantly more irradiated (UV-B, UV-C) as partially or wholly above ozone layer
- Has a sulfate aerosol layer (18–23 km)[20]:
  - supercooled sulfuric acid and water
  - acid weight fraction 0.6–0.85[21]
  - aerosol size 0.1–1 µm
- $< 10^2$–$10^5 \frac{\text{cell}}{\text{m}^3}$ recovered viable, up to 40 km[22]
- Viable cells are inactive: hardy, dormant surface survivors of desiccation, irradiation, etc.

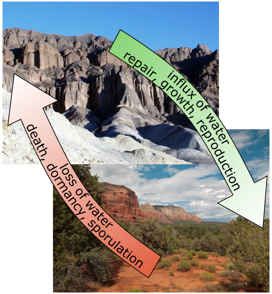
What we *don't* see is also important

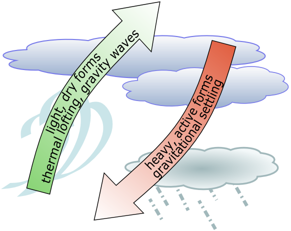
- most viable airborne microbes recovered are dormant (including all stratospheric samples)
- metabolic activity appears limited to warmest and wettest regimes (clouds a.k.a. mobile water 'hot spots')
- reproduction while airborne not yet observed *in situ*
- stratosphere is *extremely* understudied
  - platform (aircraft, balloon) limitations
  - detection and analysis challenges for sparse, patchy, spore-like forms



Reported high-altitude bioaerosol concentrations.

What are the requirements for a self-sustaining aerobiosphere?





- “hard” habitability requirements:
  - solvent (water)
  - nutrients (CHNOPS+)
  - energy (chem, light)
  - environment (rad, temp)
- “soft” habitability constraints:
  - biosphere stability requires that population growth outpace population loss in the long run
  - sporadic growth, low biomass: think “desert bloom”
- uniquely for aerobiology, residence time limitations convert the latter into the former: $t_r > t_g$
  - t_r: gravity, density, viscosity, thermal lofting, gravity waves, precipitation, turbulence...
  - t_g: slow growth or periods of inactivity: low water, nutrients, or energy, or high stress

Solvent availability (water)

- Earth's atmosphere is dry compared to most surface habitats → dependence on clouds
- rapid desiccation is the main driver of Earth's airborne microbial population loss[30]
- tropospheric cloud lifetimes are on par with microbial generation times → too transient for continuous habitation and/or adaptation?

Earth

Phenomenon	a_w
Microbial growth media	0.996
NaCl solubility	0.74
Microbial growth	≤0.6
Earth's atmosphere (mean)	0.4
Atacama desert soils	0.01–0.52

Venus

- What is the water activity of Venus's aerosols?
- How variable is that water (e.g., influx from volcanism)?
- How does this compare to residence times?

Nutrients & energy

- *bioavailable* CHNOPS (+Fe, others) are required for terrestrial-like biochemistry
- atmospheric levels typically governed by surface fluxes and mixing dynamics
- on Earth, fog/cloud water nutrient levels are similar to oligotrophic lakes (limiting!)
- energy available to autotrophs can be photonic, chemical, or both
- Earth airborne life not limited by photonic energy (more likely to have too much)

Earth

Species	**Cloud Water ($\frac{g}{L}$)**	**Lake Water ($\frac{g}{L}$)**
DOC	$0.3 - 6 \times 10^{-3}$	$1 - 5 \times 10^{-3}$
NH_4^+	$0.3 - 2 \times 10^{-2}$	2×10^{-5}
NO_2^-	$0.03 - 2 \times 10^{-3}$	6×10^{-6}
NO_3^-	$2 - 6 \times 10^{-3}$	$0.7 - 3 \times 10^{-5}$
P_3^-	$0.02 - 1 \times 10^{-4}$	$2 - 7 \times 10^{-5}$
SO_4^{-2}	6×10^{-2}	1×10^{-3}

Venus

- What is the composition of Venus's aerosols (C, N, P)?
- How does this change (daily, seasonally, long-term)?
- What are typical growth rates for potential analogue species under similar limits?

Environment (stress)

- non-optimal environments may cause slower microbial growth
- alternating between survival and growth ranges may cause periods of inactivity → short-term cycles of inactivity can be particularly challenging!
- on Earth, limited by temperature (too cold) and radiation (especially UV-C)
- on Venus, acidity (acid activity, beyond pH) is a major potential constraint[31]; closest natural analogues are uninhabited, but are also hot and saline[32;33]

Earth

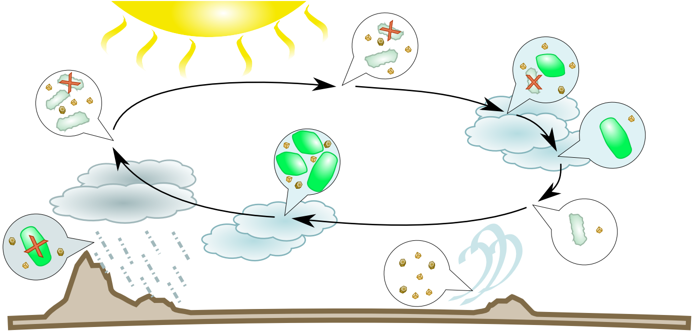
Stressor	Microbial Growth Limits	Microbial Activity Limits
T (°C)	$-12 - 121$	$< -40 - 121$
p (kPa)	$5 - 1 \times 10^5$	$\sim 2.5 - 1.3 \times 10^5$
pH	$\sim 0 - 12$	$-0.06 - 12.5$
a_w	$0.6 - \sim 1$	$\leq 0.6 - \sim 1$
UV A/B ($\frac{\mathrm{W}}{\mathrm{m}^2}$)	$0 - < 30\text{–}50$	$0 - \geq 50$

Venus

- What is the acid activity of Venus's aerosols?
- How does this change (daily, seasonally, long-term)?
- What are the limiting combinations of stressors?

All of these constraints interact!

- cloud formation affected by temperature, pressure, nucleation, etc.
- microbes that tolerate aerosolization are often condensation nuclei[34]
- very high acid activity = low water activity
- longer residence times (less vertical cycling) may mean lower nutrients
- lower temperatures reduce both damage accumulation and growth rates
- on Earth, the warmest and wettest regimes are also the shortest-lived



What would we like to see going forward?

Earth aerobiology science targets

- Determine if microbial reproduction occurs while airborne
- Characterize the stratosphere as a potential analogue environment – is microbial activity limited to clouds and/or the troposphere?
- Characterize life cycles, growth rates, and limiting combinations of stressors for potential analogue microbes (dry, acid, hot...)
- Improve *in situ* analysis instruments for "rare and tough" microbial forms

Venus *in situ* science targets

- Measure detailed aerosol composition and differentiate by particle size
- Determine water activity and acid activity (and/or major factors affecting it)
- Characterize mixing and lofting dynamics → understand particle 'life cycles'

Acknowledgments

Funding & Other Support

- NASA Ames Science Innovation Fund
- A. Sorooshian (University of Arizona)
- D. Fernandez (California State University, Monterey Bay)
- P. Weiss (University of California, Santa Cruz)

Thanks to...

- D. Smith and S. Waters
- L. Iraci, E. Barth, K. McGouldrick, K.-L. Jessup & N. Izenberg
- R. Quinn and A. Ricco
- S. Palacios

Questions?

or e-mail diana.gentry@nasa.gov

(supplementary & reference slides following)

Water activity, part 1

Water availability goes beyond molarity, pH, or salinity

- gravitational potential
- internal and external physical pressures
- partial molar water volume
- matric effects (adsorption and capillary effects from surfaces)
- osmotic balance

Combined metric: water potential (ψ) or water activity (a_w)

- Related by $\psi V_w = \mu_w - \mu_w^\circ = RT \ln a_w$
- Pure water has a ψ of 0 Pa and an a_w of 1.
- Osmotic and matric effects dominate on microbial scales.[35;36]
- At low matric potentials, gas phase interactions become limiting before osmotic potentials.[36;37]

Water activity, part 2

$$\psi V_w = \mu_w - \mu_w^\circ = RT \ln a_w$$

ψ = water potential, $\frac{\mathrm{J}}{\mathrm{m}^3}$ or Pa
V_w = partial molar volume of water in the system, $\frac{\mathrm{m}^3}{\mathrm{mol}}$
μ_w = free energy of water in the system, $\frac{\mathrm{J}}{\mathrm{mol}}$
μ_w° = free energy of reference water quantity, $\frac{\mathrm{J}}{\mathrm{mol}}$
R = ideal gas constant, 8.315 $\frac{\mathrm{J}}{\mathrm{mol \cdot K}}$
T = temperature, K
a_w = water activity, dimensionless ratio

Water spontaneously flows from an area of higher water potential to an area of lower water potential[38].
Maintaining a ψ differential costs energy, so microbes counterbalance one source of ψ difference with another to achieve equilibrium.

Some characteristic water activities

Venus's aerosols (assuming $\geq 75\,\%$ sulfuric acid) are akin to Earth's most barren deserts in a_w.

Phenomenon	ψ **(Pa)**	a_w	**Cite**
Microbial growth media	$\sim -2\times10^5$	0.996	[35;39]
Non-xerophile growth	-5×10^6		[37]
Bacterial growth(?)	-1.7×10^7		[37]
NaCl solubility	-4.1×10^7	0.74	[40]
Archean growth(?)		0.5–0.7	[41]
Don Juan Pond		0.45	[39]
$MgCl_2$ solubility		0.3	[41]
Atacama desert soils	$< -1.5\times10^8$	0.01–0.52	[40;42]
75% H_2SO_4 solution		0.02	[43]

Some characteristic rainwater nutrient levels

Typical Earth rain and fog water is akin to some oligotrophic lakes, meaning that nutrients would be limiting over time.

Species	**Cloud Water ($\frac{g}{L}$)**	**Cite**	**Lake Water ($\frac{g}{L}$)**	**Cite**
DOC	$0.3-6\times10^{-3}$	[44;45] [a]	$1-5\times10^{-3}$	[46;47] [b]
NH_4^+	$0.3-2\times10^{-2}$	[44;48]	2×10^{-5}	[49]
NO_2^-	$0.03-2\times10^{-3}$	[44;48]	6×10^{-6}	[49]
NO_3^-	$2-6\times10^{-3}$	[44;48]	$0.7-3\times10^{-5}$	[49;50]
P_3^-	$0.02-1\times10^{-4}$	[51] [c]	$2-7\times10^{-5}$	[47;50]
SO_4^{-2}	6×10^{-2}	[48]	1×10^{-3}	[52]

[a] Dissolved organic carbon; continental $>$ marine precipitation.

[b] Inhabited subsurface aquifers are $< 0.1\,\frac{mg}{L}$ [36].

[c] Typically occurs as phosphates.

Some characteristic microbial growth and reproduction limits

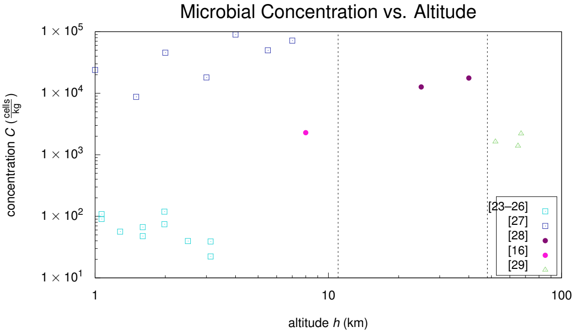
Stressor	Microbial Growth Limits	Cite	Microbial Activity Limits	Cite
temperature (°C)	$-12 - 121$	[53;54]	$< -40 - 121$	[54]
pressure (kPa)	$5 - 1 \times 10^5$	[55;56]	$\sim 2.5 - 1.3 \times 10^5$	[54;55]
pH	$\sim 0 - 12$	[57;58]	$-0.06 - 12.5$	[53;58]
water activity (a_w)	$0.6 - \sim 1$	[39;41]	$\lesssim 0.6 - \sim 1$	[39;41]
UV A&B ($\frac{\mathrm{W}}{\mathrm{m}^2}$)	$0 - < 30\text{–}50$	[59] [a]	$0 - \geq 50$	[59] [a]
PAR ($\frac{\mu\mathrm{mol}_\gamma}{\mathrm{m}^2 \cdot \mathrm{s}}$)	$\geq 1 \times 10^{-2} - 8 \times 10^3$	[60]	$\sim 1 \times 10^{-2} - 8 \times 10^3$	[60]

[a] Empirical value for a typical high-altitude terrestrial habitat.

The state of aerobiological knowledge is coarse

Platform limitations are significant.

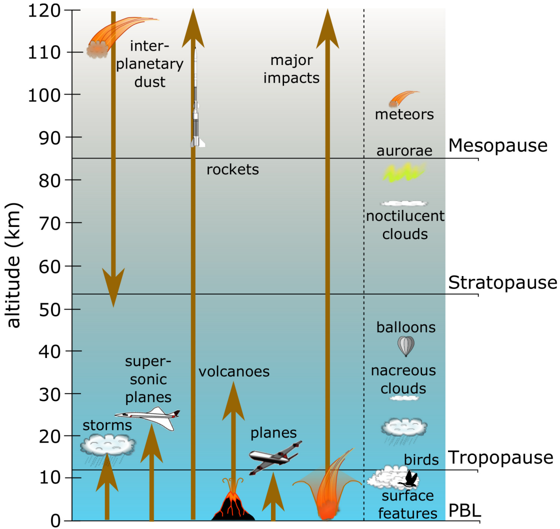
- ground (< 10 m) is dominated by transient bioaerosols
- towers (< 100 m) yields single points
- higher-altitude sampling with aircraft gives 1D transects
- higher-altitude samples are extremely scarce and ad hoc
- questions about metabolic activity, stress responses, and potential life cycles require fine-scale, 4D samples



Reported high-altitude bioaerosol concentrations (arithmetic mean). Square markers indicate airplane sampling, circles balloons, and triangles sounding rockets. Open markers indicate culture-dependent analyses, solids culture-independent counts.

Stratospheric sampling lessons

- Nearly all biomass is dead/dormant: different signatures, ‘tough to crack’
- Low biomass & very patchy distributions → need to concentrate sample in time and space
- Passive platforms (balloons) follow the same airmass → may miss hotspots
- Sample starts changing immediately after capture (temp, ionization, phase...)
- Spectral measurements require very good *a priori* baselines
- Most reliable measurements come from sample return (e.g., sequencing)



References I

[1] M. J. Way and Anthony D. Del Genio. Venusian Habitable Climate Scenarios: Modeling Venus Through Time and Applications to Slowly Rotating Venus-Like Exoplanets. *Journal of Geophysical Research: Planets*, 125(5):e2019JE006276, 2020.

[2] Sanjay S. Limaye, Rakesh Mogul, David J. Smith, Arif H. Ansari, Grzegorz P. Słowik, and Parag Vaishampayan. Venus' Spectral Signatures and the Potential for Life in the Clouds. *Astrobiology*, 18(9):1181–1198, March 2018.

[3] Jane S. Greaves, Anita M. S. Richards, William Bains, Paul B. Rimmer, Hideo Sagawa, David L. Clements, Sara Seager, Janusz J. Petkowski, Clara Sousa-Silva, Sukrit Ranjan, Emily Drabek-Maunder, Helen J. Fraser, Annabel Cartwright, Ingo Mueller-Wodarg, Zhuchang Zhan, Per Friberg, Iain Coulson, E'lisa Lee, and Jim Hoge. Phosphine gas in the cloud decks of Venus. *Nature Astronomy*, September 2020.

[4] C. J. Bierson and X. Zhang. Chemical Cycling in the Venusian Atmosphere: A Full Photochemical Model From the Surface to 110 km. *Journal of Geophysical Research: Planets*, 125(7):e2019JE006159, 2020.

[5] Robert M Bowers, Shawna McLetchie, Rob Knight, and Noah Fierer. Spatial variability in airborne bacterial communities across land-use types and their relationship to the bacterial communities of potential source environments. *The ISME Journal*, 5(4):601–612, April 2011.

References II

[6] S. M. Burrows, W. Elbert, M. G. Lawrence, and U. Pöschl. Bacteria in the global atmosphere – Part 1: Review and synthesis of literature data for different ecosystems. *Atmospheric Chemistry and Physics*, 9(23):9263–9280, December 2009.

[7] R. Jaenicke. Abundance of Cellular Material and Proteins in the Atmosphere. *Science*, 308(5718):73–73, April 2005.

[8] Pierre Amato, Marius Parazols, Martine Sancelme, Gilles Mailhot, Paolo Laj, and Anne-Marie Delort. An important oceanic source of micro-organisms for cloud water at the Puy de Dôme (France). *Atmospheric Environment*, 41(37):8253–8263, December 2007.

[9] Pierre Amato, Muriel Joly, Ludovic Besaury, Anne Oudart, Najwa Taib, Anne I. Moné, Laurent Deguillaume, Anne-Marie Delort, and Didier Debroas. Active microorganisms thrive among extremely diverse communities in cloud water. *PloS one*, 12(8):e0182869, 2017.

[10] Kevin P. Dillon, Florence Correa, Celine Judon, Martine Sancelme, Donna E. Fennell, Anne-Marie Delort, and Pierre Amato. Cyanobacteria and algae in clouds and rain in the area of Puy de Dôme, Central France. *Applied and Environmental Microbiology*, 87(1):e01850–20, Oct 2020.

[11] Eoin L. Brodie, Todd Z. DeSantis, Jordan P. Moberg Parker, Ingrid X. Zubietta, Yvette M. Piceno, and Gary L. Andersen. Urban aerosols harbor diverse and dynamic bacterial populations. *Proceedings of the National Academy of Sciences*, 104(1):299–304, 2007.

References III

[12] Andrew C. Schuerger, David J. Smith, Dale W. Griffin, Daniel A. Jaffe, Boris Wawrik, Susannah M. Burrows, Brent C. Christner, Cristina Gonzalez-Martin, Erin K. Lipp, David G. Schmale III, and Hongbin Yu. Science questions and knowledge gaps to study microbial transport and survival in Asian and African dust plumes reaching North America. *Aerobiologia*, 34(4):425–435, December 2018.

[13] Hans W. Paerl and J. L. Pinckney. A mini-review of microbial consortia: Their roles in aquatic production and biogeochemical cycling. *Microbial Ecology*, 31(3):225–247, 1996.

[14] Marian L. Yallop, Alexandre M. Anesio, Rupert G. Perkins, Joseph Cook, Jon Telling, Daniel Fagan, James MacFarlane, Marek Stibal, Gary Barker, Chris Bellas, et al. Photophysiology and albedo-changing potential of the ice algal community on the surface of the Greenland ice sheet. *The ISME journal*, 6(12):2302–2313, 2012.

[15] H. E. Ahern, K. A. Walsh, T. C. J. Hill, and B. F. Moffett. Fluorescent pseudomonads isolated from Hebridean cloud and rain water produce biosurfactants but do not cause ice nucleation. *Biogeosciences*, 4(1):115–124, 2007.

[16] Kerri A. Pratt, Paul J. DeMott, Jeffrey R. French, Zhien Wang, Douglas L. Westphal, Andrew J. Heymsfield, Cynthia H. Twohy, Anthony J. Prenni, and Kimberly A. Prather. In situ detection of biological particles in cloud ice-crystals. *Nature Geoscience*, 2(6):398–401, June 2009.

References IV

[17] B. C. Christner, C. E. Morris, C. M. Foreman, R. Cai, and D. C. Sands. Ubiquity of Biological Ice Nucleators in Snowfall. *Science*, 319(5867):1214–1214, February 2008.

[18] Parisa A. Ariya, Oleg Nepotchatykh, Olga Ignatova, and Marc Amyot. Microbiological degradation of atmospheric organic compounds. *Geophysical Research Letters*, 29(22):34–1–34–4, November 2002.

[19] Anne-Marie Delort, Mickael Vaïtilingom, Pierre Amato, Martine Sancelme, Marius Parazols, Gilles Mailhot, Paolo Laj, and Laurent Deguillaume. A short overview of the microbial population in clouds: Potential roles in atmospheric chemistry and nucleation processes. *Atmospheric Research*, 98(2-4):249–260, November 2010.

[20] D. J. Hofmann and J. M. Rosen. On the Background Stratospheric Aerosol Layer. *Journal of the Atmospheric Sciences*, 38(1):168–181, January 1981.

[21] G. K. Yue, L. R. Poole, P.-H. Wang, and E. W. Chiou. Stratospheric aerosol acidity, density, and refractive index deduced from SAGE II and NMC temperature data. *Journal of Geophysical Research: Atmospheres*, 99(D2):3727–3738, 1994.

[22] N. C. Bryan, B. C. Christner, T. G. Guzik, D. J. Granger, and M. F. Stewart. Abundance and survival of microbial aerosols in the troposphere and stratosphere. *The ISME Journal*, 13(11):2789–2799, November 2019.

References V

[23] John D. Fulton. Microorganisms of the upper atmosphere III. Relationship between altitude and micropopulation. *Applied microbiology*, 14(2):237–240, 1966.

[24] John D. Fulton. Microorganisms of the Upper Atmosphere IV. Microorganisms of a Land Air Mass as it Traverses an Ocean. *Applied Microbiology*, 14(2):241–244, 1966.

[25] John D. Fulton. Microorganisms of the upper atmosphere V. Relationship between frontal activity and the micropopulation at altitude. *Applied microbiology*, 14(2):245–250, 1966.

[26] John D. Fulton and Roland B. Mitchell. Microorganisms of the Upper Atmosphere II. Microorganisms in Two Types of Air Masses at 690 Meters Over a City. *Applied Microbiology*, 14(2):232–236, 1966.

[27] Irina S. Andreeva, Alexander I. Borodulin, Galina A. Buryak, Vladidmir A. Zhukov, Sergei V. Zykov, Yuri V. Marchenko, Victor V. Marchenko, Sergei E. Olkin, Valentina A. Petrishchenko, Oleg V. Pyankov, Irina K. Reznikova, Vladimir E. Repin, Alexander S. Safatov, Alexander N. Sergeev, Vladimir F. Raputa, Vladidmir V. Penenko, Eleva A. Tsvetova, Mikhail Yu. Arshinov, Boris D. Belan, Mikhail V. Panchenko, Alexander N. Ankilov, Anatoli M. Baklanov, Alexander L. Vlasenko, Konstantin P. Koutsenogii, Valery I. Makarov, and Tatiana V. Churkina. Biogenic Component of Atmospheric Aerosol in the South of West Siberia. *Chemistry for Sustainable Development*, 10:523–537, 2002.

References VI

[28] Melanie J. Harris, Nalin C. Wickramasinghe, David Lloyd, J. V. Narlikar, P. Rajaratnam, Michael P. Turner, Shirwan Al-Mufti, Max K. Wallis, S. Ramadurai, and Fred Hoyle. Detection of living cells in stratospheric samples. In Richard B. Hoover, Gilbert V. Levin, Roland R. Paepe, and Alexei Y. Rozanov, editors, *International Symposium on Optical Science and Technology*, pages 192–198, San Diego, CA, February 2002.

[29] A A Imshenetsky, S V Lysenko, and G A Kazakov. Upper Boundary of the Biosphere. *Applied and Environmental Microbiology*, 35(1):1–5, 1978.

[30] Alan Jeff Mohr. Fate and Transport of Microorganisms in Air. In *Manual of Environmental Microbiology, Third Edition*, pages 961–971. ASM Press, Washington, D.C., 3rd edition, January 2007.

[31] S Seager, J J Petkowski, P Gao, W Bains, N C Bryan, S Ranjan, and J Greaves. The Venusian Lower Atmosphere Haze as a Depot for Desiccated Microbial Life: A Proposed Life Cycle for Persistence of the Venusian Aerial Biosphere. *Astrobiology*, page 34, 2020.

[32] Felipe Gómez, Barbara Cavalazzi, Nuria Rodríguez, Ricardo Amils, Gian Gabriele Ori, Karen Olsson-Francis, Cristina Escudero, Jose M. Martínez, and Hagos Miruts. Ultra-small microorganisms in the polyextreme conditions of the Dallol volcano, Northern Afar, Ethiopia. *Scientific Reports*, 9(11):7907, May 2019.

References VII

[33] Jodie Belilla, David Moreira, Ludwig Jardillier, Guillaume Reboul, Karim Benzerara, José M. López-García, Paola Bertolino, Ana I. López-Archilla, and Purificación López-García. Hyperdiverse archaea near life limits at the polyextreme geothermal Dallol area. *Nature Ecology & Evolution*, 3(11):1552–1561, November 2019.

[34] Pascal Renard, Isabelle Canet, Martine Sancelme, Nolwenn Wirgot, Laurent Deguillaume, and Anne-Marie Delort. Screening of cloud microorganisms isolated at the Puy de Dôme (France) station for the production of biosurfactants. *Atmospheric Chemistry and Physics*, 16(18):12347–12358, Sep 2016.

[35] R. F. Harris. Effect of Water Potential on Microbial Growth and Activity. In *Water Potential Relations in Soil Microbiology*, pages 23–95. Soil Science Society of America, January 1981.

[36] Thomas L. Kieft. Survival of Microorganisms in Subsurface Sediments. In Gabriel Bitton, editor, *Encyclopedia of Environmental Microbiology*. John Wiley & Sons, Inc., Hoboken, NJ, USA, January 2003.

[37] M. Potts. Desiccation tolerance of prokaryotes. *Microbiological Reviews*, 58(4):755–805, December 1994.

[38] R. I. Papendick and G. S. Campbell. Theory and Measurement of Water Potential. In *Water Potential Relations in Soil Microbiology*, pages 1–22. Soil Science Society of America, 1981.

[39] W. D. Grant. Life at low water activity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 359(1448):1249–1267, August 2004.

References VIII

[40] Stephanie A. Connon, Elizabeth D. Lester, Hannah S. Shafaat, Donald C. Obenhuber, and Adrian Ponce. Bacterial diversity in hyperarid Atacama Desert soils. *Journal of Geophysical Research: Biogeosciences*, 112(G4):S17, December 2007.

[41] Henk Bolhuis, Peter Palm, Andy Wende, Michaela Falb, Markus Rampp, Francisco Rodriguez-Valera, Friedhelm Pfeiffer, and Dieter Oesterhelt. The genome of the square archaeon *Haloquadratum walsbyi*: Life at the limits of water activity. *BMC Genomics*, 7(1):1, 2006.

[42] Thomas L. Kieft. Desert environments: Soil microbial communities in hot deserts. In Gabriel Bitton, editor, *Encyclopedia of Environmental Microbiology*, pages 1–25. John Wiley & Sons, Inc., Hoboken, NJ, USA, January 2003.

[43] N. C. Deno and R. W. Taft. Concentrated Sulfuric Acid-Water. *Journal of the American Chemical Society*, 76(1):244–248, January 1954.

[44] A Marinoni, P Laj, K Sellegri, and G Mailhot. Cloud chemistry at the puy de dôme: variability and relationships with environmental factors. *Atmospheric Chemistry and Physics Discussions*, 4:849–886, 2004.

[45] Joan D. Willey, Robert J. Kieber, Mary S. Eyman, and G. Brooks Avery. Rainwater dissolved organic carbon: Concentrations and global flux. *Global Biogeochemical Cycles*, 14(1):139–148, Mar 2000.

References IX

[46] Jonathan J. Cole, William H. McDowell, and Gene E. Likens. Sources and molecular weight of "dissolved" organic carbon in an oligotrophic lake. *Oikos*, 42(1):1, Jan 1984.

[47] L Forsström, T Roiha, and M Rautio. Responses of microbial food web to increased allochthonous dom in an oligotrophic subarctic lake. *Aquatic Microbial Ecology*, 68(2):171–184, Mar 2013.

[48] Sandro Fuzzi, Paolo Mandrioli, and Antonio Perfetto. Fog droplets—an atmospheric source of secondary biological aerosol particles. *Atmospheric Environment*, 31(2):287–290, Jan 1997.

[49] A. J. Horne and D. L. Galat. Nitrogen fixation in an oligotrophic, saline desert lake: Pyramid lake, nevada: N 2 fixation in pyramid lake. *Limnology and Oceanography*, 30(6):1229–1239, Nov 1985.

[50] Charles R Goldman. Primary productivity, nutrients, and transparency during the early onset of eutrophication in ultra-oligotrophic lake tahoe, california-nevada. *Limnology and Oceanography*, 33(6):1321–1333, 1988.

[51] Christophe Migon and Valérie Sandroni. Phosphorus in rainwater: Partitioning inputs and impact on the surface coastal ocean. *Limnology and Oceanography*, 44(4):1160–1165, Jun 1999.

[52] Marianne Holmer and Peter Storkholm. Sulphate reduction and sulphur cycling in lake sediments: a review. *Freshwater Biology*, 46(4):431–451, Apr 2001.

References X

[53] Nancy Merino, Heidi S. Aronson, Diana P. Bojanova, Jayme Feyhl-Buska, Michael L. Wong, Shu Zhang, and Donato Giovannelli. Living at the Extremes: Extremophiles and the Limits of Life in a Planetary Context. *Frontiers in Microbiology*, 10, 2019.

[54] Shawn D. Domagal-Goldman, Katherine E. Wright, Katarzyna Adamala, Leigh Arina de la Rubia, Jade Bond, Lewis R. Dartnell, Aaron D. Goldman, Kennda Lynch, Marie-Eve Naud, Ivan G. Paulino-Lima, and et al. The astrobiology primer v2.0. *Astrobiology*, 16(8):561–653, Aug 2016.

[55] Wayne L. Nicholson, Patricia Fajardo-Cavazos, Jeffrey Fedenko, José L. Ortíz-Lugo, Andrea Rivas-Castillo, Samantha M. Waters, and Andrew C. Schuerger. Exploring the Low-Pressure Growth Limit: Evolution of *Bacillus subtilis* in the Laboratory to Enhanced Growth at 5 Kilopascals. *Applied and Environmental Microbiology*, 76(22):7559–7565, November 2010.

[56] Chiaki Kato, Lina Li, Yuichi Nogi, Yuka Nakamura, Jin Tamaoka, and Koki Horikoshi. Extremely barophilic bacteria isolated from the Mariana Trench, Challenger Deep, at a depth of 11,000 meters. *Applied and Environmental Microbiology*, 64(4):1510–1513, 1998.

[57] Brett J. Baker and Jillian F. Banfield. Microbial communities in acid mine drainage. *FEMS Microbiology Ecology*, 44(2):139–152, May 2003.

References XI

[58] C Schleper, G Puehler, I Holz, A Gambacorta, D Janekovic, U Santarius, H P Klenk, and W Zillig. *Picrophilus* gen. nov., fam. nov.: a novel aerobic, heterotrophic, thermoacidophilic genus and family comprising archaea capable of growth around ph 0. *Journal of Bacteriology*, 177(24):7050–7059, 1995.

[59] YongQin Liu, TanDong Yao, ShiChang Kang, NianZhi Jiao, YongHui Zeng, SiJun Huang, and TingWei Luo. Microbial community structure in major habitats above 6000 m on Mount Everest. *Chinese Science Bulletin*, 52(17):2350–2357, September 2007.

[60] J.A. Raven and C.S. Cockell. Influence on photosynthesis of starlight, moonlight, planetlight, and light pollution (reflections on photosynthetically active radiation in the universe). *Astrobiology*, 6(4):668–675, Aug 2006.