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Current Opinion in Microbiology

Survival of microbes in Earth's stratosphere

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The remarkable survival of microorganisms high above the surface of the Earth is of increasing interest. At stratospheric levels, multiple stressors including ultraviolet and ionizing radiation, low temperatures, hypobaric conditions, extreme desiccation, and nutrient scarcity are all significant challenges. Our understanding of which microorganisms are capable of tolerating such stressful conditions has been addressed by stratospheric sample collection and survival assays, through launching and recovery, and exposure to simulated conditions in the laboratory. Here, we review stratospheric microbiology studies providing our current perspective on microbial life at extremely high altitudes and discuss implications for health and agriculture, climate change, planetary protection, and astrobiology.

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Current Opinion in Microbiology 2018, **43**:24–30

This review comes from a themed issue on **Environmental microbiology**

Edited by **Alberto Scoma** and **Julia Vorholt**

https://doi.org/10.1016/j.mib.2017.11.002

Introduction

While the atmosphere represents the largest fraction of the biosphere by volume, it contains by far the lowest number of cells. Estimates have suggested that the atmosphere, primarily the troposphere (<5 to 18 km above sea level), contains less than a billionth the number of cells found in the oceans, soils, and subsurface [1]. At stratospheric elevations, from 12–18 km to 50 km above sea level, the number of cells declines and temperature, oxygen, and humidity levels all plummet (Figure 1). Above the ozone layer (~15 to 35 km), ultraviolet (UV) and cosmic radiation quickly become lethal factors (Box 1). At even higher elevations, above 50 km, into the mesosphere and thermosphere, life as we know it may be impossible.

Microorganisms of terrestrial origin enter the stratosphere by vertical movement of air from the troposphere as a result of thunderstorms, dust storms, volcanic action, and human activity (Box 2). Over 10^{21} cells are lifted annually into the atmosphere, leading to considerable transport and dispersal around the globe, even with a very small fraction (<0.1%) surviving due to the extreme conditions [1,2,3•]. Exact cell counts in the stratosphere are yet to be fully established, but some sporulating and non-sporulating bacteria and fungi are regularly recovered (Table 1). Moreover, certain widely distributed species, such as extremophilic archaea and pathogenic bacteria, have been shown to survive residency in the stratosphere, at least for short periods of time [4••,5••].

Microbes isolated from the stratosphere

Early sampling expeditions revealed that the upper limit of terrestrial life is at a very high altitude, above the troposphere, in the stratosphere, or possibly even higher [6]. In 1936, Rogers and Meyer reported the first successful air sampling mission reaching the stratosphere (11–21 km). Using balloons with autoclaved collection tubes, they isolated both viable bacteria and fungi, including *Bacillus* and *Aspergillus* spp. (Table 1). In 1965, Soffen reported isolating only *Penicillium* sp. using an impactor which had been sterilized by ethylene oxide for air sampling at 40 km also using balloons. In the 1970s, Imshenetsky and co-workers sampled air from 48 to 85 km elevation using meteorological rockets sterilized by γ-radiation. Remarkably, isolates were reported up to 77 km, and primarily the same types of fungi as previously reported in stratospheric sampling. In addition, the non-spore forming *Micrococcus albus* and *Mycobacterium luteum* bacteria were also found (Table 1).

In more recent sampling expeditions, enhanced technology for sterilization of sampling devices, and culturing and non-culturing methods have been refined [7•,8–10,11••]. A balloon-borne cryosampler was used to collect material from 41 km, resulting in isolation of viable *Bacillus simplex*, *Staphylococcus pasteuri* and the fungus *Engyodontium albus* [12]. An impactor device mounted on the underside of a high altitude research aircraft at 20 km was used to collect spore-forming *Penicillium* sp., *Bacillus luciferensis* and *B. sphaericus* [13]. In a subsequent mission, non-spore-forming bacteria from the families *Micrococcaceae* and *Microbacteriaceae*, and genera *Staphylococcus* and *Brevibacterium* were isolated [14]. Interestingly, most *Micrococcaceae* and several *Microbacteriaceae* matched to previously identified strains from volcanic soils, suggesting that these may be lofted into the stratosphere during eruptions. Delayed growth and smaller colony

Figure 1

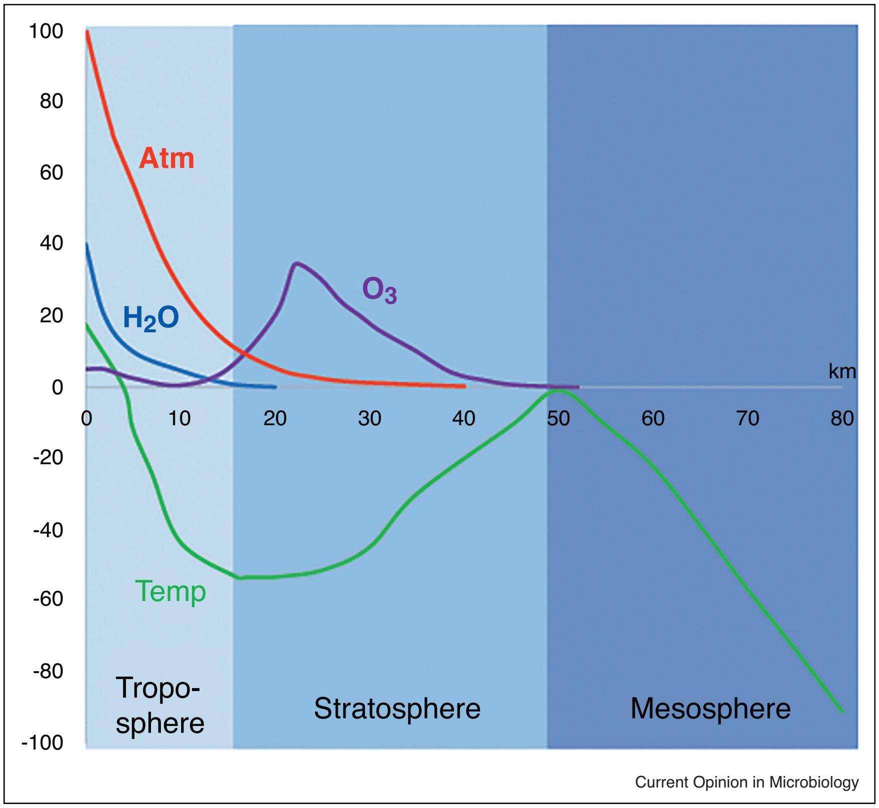

Diagram displaying characteristics of the atmosphere. Atmospheric temperature (Temp, in °C, green), atmospheric pressure (Atm, in kPa, red), water vapor (H_2O, in g/m^3, blue), and ozone (O_3, in mPa, purple) on the *Y*-axis are all plotted against elevation above sea level (ASL in km) on the *X*-axis.

Box 1 Major stratospheric stressors

- UV-C radiation
- Cosmic radiation
- Freezing temperatures
- Hypobaric pressure
- Desiccating condition
- Starvation
- Ozone

Box 2 Activities affecting the stratosphere

Human	Nature
• Commercial jet aircraft	• Volcanic eruptions
• Meteorological balloons	• Tropical storms
• Military aircraft and rockets	• Thunderstorms
• Spacecraft and satellite transit	• Dust storms

formation were noted for the isolates and attributed to cell stress [14].

In a mission to 11–12 km elevation, slow-growing microbes in the *Deinococcus* genus were isolated using an airdust sampler, and later classified as *Deinococcus aetherius*. Several *Bacillus* spp. and a *Paenibacillus* strain were also identified from the flight collections [15,16]. An aerobiology sampling mission at 20 km elevation recovered two fungi, *Penicillium* and *Eurotiomycetes*, and *Bacillus subtilis* and *B. endophyticus*, as well as a very slow-growing *Bacillus* strain, which likely originated from trans-Pacific dust (Table 1) [17]. Most recently, a microbial aerosol sampling mission cultured *Bacillus*, *Paenibacillus*, *Actinobacteria* and *Proteobacteria* [10], (NC Bryan *et al*., abstract 7523, Astrobiology Science Conference, Chicago, IL, 2015). These investigators also estimated metabolic activity from ATP measurements in biomass and suggested densities of 10^5–10^6 microbial cells/m^3 in the stratosphere.

While recent studies have clearly established that viable and diverse microorganisms are present in the stratosphere (Table 1), largely dispelling earlier sterility and