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Microorganisms of the Phyllosphere: Origin, Transport, and Ecological Functions

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Microbes are ubiquitous residents of the atmosphere, including the air that we breathe. They are also widely present in terrestrial, marine, and aquatic environments. Typical microbes include viruses, fungi, archaea, bacteria, algae, and bryophytes. Many are of edaphic origin and play significant ecological roles in the soil. Propagules are exceedingly lightweight and small, generally measured in microns (millionths of a meter). Propagules achieve airborne status in the wind, where they may travel from a few millimeters to thousands of kilometers. Most have been recorded at least as high as the stratosphere. While airborne, microbes may pass through multiple generations. Microbes in the atmosphere are often accompanied by vast clouds of dust. They perform a variety of essential functions such as raindrop and snowflake condensation nuclei, without which there would be little or no precipitation. It is important to realize that all solid things that are carried up into the atmosphere must eventually fall back down to the Earth. When precipitated or deposited back onto the Earth, they may land on and occupy any surface, including trees and other plants where they become epiphytic residents. They have been documented on broad-leaved and needle-leaved trees from deserts to tropical rainforests. If they land on bare soil, they often participate in biological soil crusts that are important for soil stabilization and for water and nutrient cycling.

Keywords: viruses, fungi, archaea, bacteria, algae, bryophytes, aerobiology

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INTRODUCTION

Microbes are nearly ubiquitous in the atmosphere, including in the air that we and other animals breathe. It has been estimated that billions of microbes are descending from the atmosphere at all times of every day (Weisberger, 2018). Typical microbes include viruses, fungi (free-living, lichenized, and mycorrhizal), archaea, bacteria (cyanobacteria, chemoheterotrophic, and diazotrophic), algae including diatoms, and bryophytes (mosses, liverworts, and stoneworts) (Koskella, 2020; Warren and St Clair, 2021). Some microbes reproduce sexually, but most rely primarily on asexual means of reproduction (Warren et al., 2019). Common forms of asexual reproduction among microorganisms include replication, fragmentation, binary fission, cloning, budding, mitotic cell division, asexual sporogenesis, etc. Many of the asexual propagules, and even some of the mature microorganisms are very small, measured in microns (millionths of a meter). Given their small size and weight, microbes and/or their propagules are easily lifted into the atmosphere (Després et al., 2012; Fröhlich-Nowoisky et al., 2016) at least as high as the stratosphere (DasSarma et al., 2020). They are dispersed aerially over extensive distances (Mayol et al., 2017;

Reche et al., 2018), including intercontinentally and interhemispherically (Prospero et al., 2005). Microbes are often accompanied by vast clouds of dust from the Earth's arid areas (Griffin, 2020; Hu et al., 2020).

As microbes and their propagules return to the Earth's surface, they may be deposited onto bare soil where they can be incorporated into biological soil crusts (Belnap and Lange, 2001). Where bare soil is absent, as in tropical rainforests, the microorganisms occupy the duff or litter layer (Tripathi et al., 2016). Deposited microbes are very abundant, ranging up to 10^7 living cells of bacteria alone per square centimeter of surface area (Lindow and Brandl, 2003). Airborne microorganisms may alternatively fall onto lava beds (Lavoie et al., 2017), mine tailings (Gypser et al., 2016), or sand dunes (Smith et al., 2004). They may land on bodies of freshwater (Benson et al., 2019) or saltwater (Ul-Hasan et al., 2019). Some may land on snow (Yakimovich et al., 2020), glaciers (Anesio et al., 2017), rocks (Coleine et al., 2021), stone monuments (Li et al., 2016), gravestones (Villanueva et al., 2019), building roofs and facades (Barberán et al., 2015), or animals (Kaup et al., 2021). Others may be inhaled by humans or other animals (Barberán et al., 2015).

Given the theme of this special issue, many microbes and/or their propagules are known to fall from the atmosphere and land on trees where they become epiphytic residents of the phyllosphere, i.e., the aboveground parts of plants exposed to the atmosphere (Koskella, 2020). It can be logically concluded that all plants have epiphytic microbes. Microorganisms have been documented on coniferous trees and shrubs (Neitlich and McCune, 1997; Sevgi et al., 2019) and broad-leaved trees and shrubs (Wallace et al., 2018; Herrmann et al., 2021), fruit trees (Michavila et al., 2017; Janakiev et al., 2019), and nut trees (Pardatscher and Schweigkofler, 2009; Valverde et al., 2017).

In addition to trees, all other plants have a phyllosphere occupied by microorganisms (Partida-Martínez and Heil, 2011), including grasses and grains (Aydogan et al., 2020; Bowsher et al., 2021), ferns (Jackson et al., 2006), vegetables, fruits, and ornamental flowers (Lopez-Velasco et al., 2011; Mamphogoro et al., 2020), as well as cacti and other desert plants (Fonseca-Garcia et al., 2016; Flores-Nuñez et al., 2020). This includes trees and other plants in all climates from tropical rain forests (Kim et al., 2012), to hyperarid deserts (Al-Ashhab et al., 2021), to frigid areas such as Antarctica (Cid et al., 2017). Epiphytic microbes are even known to occur on emergent seagrass (Agawin et al., 2016). While microbes are precipitated onto exposed tree and other plant surfaces, their arrival my vary spatially and seasonally (Lighthart, 1997; Grady et al., 2019).

FUNCTIONAL ROLES OF EPIPHYTIC MICROBES

Epiphytic microorganisms are dispersed passively by wind (Cusimano et al., 2016) and are often accompanied by great clouds of dust (Gannet Hallar et al., 2011). However, as dust particles coalesce and become heavier, and as windspeeds subside, the airborne microorganisms and accompanying dust particles are precipitated back to Earth (Itani and Smith, 2016).

Epiphytic microbes may have either positive or negative impacts on their hosts (Rastogi et al., 2013). Bacteria, fungi, and viruses are often antagonistic pathogens, although some may act as mutualists of the host, promoting plant growth and tolerance of environmental stressors (Stone et al., 2018). As an example, the bacterium *Pseudomonas syringae*, a well-known plant pathogen, is also a biocontrol against plant viruses and other plant bacteria (Passera et al., 2019). Epiphytic microorganisms also fix or consolidate plant nutrients, particularly nitrogen (Fürnkranz et al., 2008), thus promoting growth of the host plant. Phyllosphere microorganisms can promote plant growth in other ways as well (Wagi and Ahmed, 2017; Yurimoto et al., 2021). Phyllosphere bacteria may also alter susceptibility to insect herbivory (Wielkopolan and Obrępalska-Stęplowska, 2016). Others have been shown to induce tolerance to drought stress (Kumar Devarajan et al., 2021).

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

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