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Review article

Airborne bacteria in the atmosphere: Presence, purpose, and potential

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HIGHLIGHTS

- Understanding the presence of airborne bacteria in the atmosphere.
- Unravelling the roles airborne bacteria have on atmospheric processes and health.
- Exploring the underlying potential of airborne bacteria for various applications.

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ABSTRACT

Numerous recent studies have highlighted that the types of bacteria present in the atmosphere often show predictable patterns across space and time. These patterns can be driven by differences in bacterial sources of the atmosphere and a wide range of environmental factors, including UV intensity, precipitation events, and humidity. The abundance of certain bacterial taxa is of interest, not only for their ability to mediate a range of chemical and physical processes in the atmosphere, such as cloud formation and ice nucleation, but also for their implications -both beneficial and detrimental-for human health. Consequently, the widespread importance of airborne bacteria has stimulated the search for their applicability. Improving air quality, modelling the dispersal of airborne bacteria (e.g. pathogens) and biotechnological purposes are already being explored. Nevertheless, many technological challenges still need to be overcome to fully understand the roles of airborne bacteria in our health and global ecosystems.

1. Introduction

When a beam of light is shone in a darkened room, it illuminates the particles in its path, reminding us that air consists of more than just gases. Beyond the visible particles, lies an airborne ecosystem teeming with microorganisms. From 1860, when airborne microbes were first systemically studied by Louis Pasteur (Pasteur, 1861), they have intrigued scientists not only with their presence, but also with their purpose. The advent of DNA-based molecular tools served to push the field forward, by no longer being limited to the very small fraction of culturable microbes (Gandolfi et al., 2013). Intriguingly, using DNA-based methods, bacterial communities in the outdoor atmosphere appear to show a diversity approximating soil and aquatic environments (Brodie et al., 2007; Katra et al., 2014; Maron et al., 2005). Over the last decade, the number of studies in this field are steadily increasing. These studies have revealed the unique and prominent roles airborne bacteria may have on atmospheric processes (Delort et al., 2010; Morris et al., 2011) and human health (Degobbi et al., 2011; Liebers et al., 2008). However, what is less explored is the underlying potential of airborne bacteria for various applications. This review will address the aspects that govern outdoor airborne bacteria (such as their sources, dispersal, survival, and factors influencing their metabolism), their impacts on human health, and their role in regional and global climate feedback mechanisms. These aspects illustrate the versatile importance of the bacteria in the atmosphere and allow insight in possible applications of these organisms.

2. Airborne bacteria in the atmosphere

2.1. Sources

Bacteria enter the near-surface atmosphere by aerosolization

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from various surfaces exposed to air currents. Jones and Harrison (2004) state that bacteria from soil and plant surfaces are released into the atmosphere based on the theory of particle resuspension processes. Their theory is supported by several observations. Firstly, several studies show a correlation between land cover and near-surface atmospheric concentrations of bacteria including those by Bertolini et al. (2013), Shaffer and Lighthart (1997), and Tong and Lighthart (2000). Secondly, so-called 'source-tracking studies' allow an estimation of the relative contribution of the sources of airborne bacteria at a particular location. The taxonomic identifications of airborne organisms are used to determine contribution of the putative source environments, in which these taxonomic units are typically found (Bowers et al., 2011a, 2011b; Cao et al., 2014). Thirdly, upward bacterial fluxes from soil and vegetation can be measured (as reviewed by Burrows et al. (2009b)). For instance, Lighthart and Shaffer (1994) measured a maximum flux of 17,000 colony forming units $m^{-2}\ h^{-1}$ above a desert-like scrubland. Moreover, they showed that the upward bacterial flux is correlated with the intensity of sensible heat, which can be explained by its role in upward convective air movements. Besides soil and vegetation, oceans and seas are also known to contribute to the bacterial content of the atmosphere by ejection of aerosol droplets into the air (Aller et al., 2005). Other potential sources of airborne bacteria have been identified, as illustrated in Fig. 1. The relative contribution of these sources varies greatly and dominant sources tend to change with time and space.

2.2. Dispersal

Bacteria can persist in the atmosphere as individual cells or can be associated with other particles, such as soil dust, leaf fragments, spores or other microorganisms (Lighthart, 1997; Maki et al., 2008; Maron et al., 2005; Tong and Lighthart, 2000). Once aerosolized, bacteria can be transported upwards by convective air movements and, due to their small size, they can remain in the atmosphere for a significant period of time. In fact, intercontinental transport has been observed, including transport of bacteria associated with dust plumes originating from deserts and drought stricken areas (Barberán et al., 2014; Hara and Zhang, 2012; Kellogg and Griffin, 2006; Lim et al., 2011; Polymenakou et al., 2008). These dust events are known to cause great changes in the downwind atmospheric bacterial community (Maki et al., 2013). For instance, the bacteria associated with the desert dust were shown to easily outnumber the local atmospheric bacteria 10 to 1 at a downwind location over 1000 km from the source (Jeon et al., 2011). Travelling dust plumes may also accumulate other bacteria on their way, for example, marine bacteria when travelling over oceans or seas. (Kellogg and Griffin, 2006; Maki et al., 2013). In addition to dust plumes, tropical storms or transportation higher into the troposphere may assist in long range transport of airborne bacteria (Burrows et al., 2009a; DeLeon-Rodriguez et al., 2013; Stres et al., 2013). An increasing number of studies on airborne microbes are supported with backward trajectory modelling that allows a better insight as to where the airborne microbes originated, such as those by Bottos et al. (2014), Fahlgren et al. (2010), Lee et al. (2007), and Murata and Zhang (2014). These studies also show that long-distance transport by normal wind patterns can contribute greatly to the bacterial composition of a local atmosphere.

2.3. Deposition

Bacteria are eventually removed from the atmosphere by either "dry" deposition or "wet" deposition (Jones et al., 2008). Dry deposition is explained by adherence to buildings, plants, water surfaces, the ground and other surfaces in contact with the air (Jones and Harrison, 2004; Jones et al., 2008). The wet deposition of bacteria is caused by the precipitation of rain, snow or hail that has collected atmospheric particles (Christner et al., 2008a; Jones et al., 2008; Monteil et al., 2014; Peter et al., 2014). In some cases, wet deposition can be actively induced by the bacteria themselves,

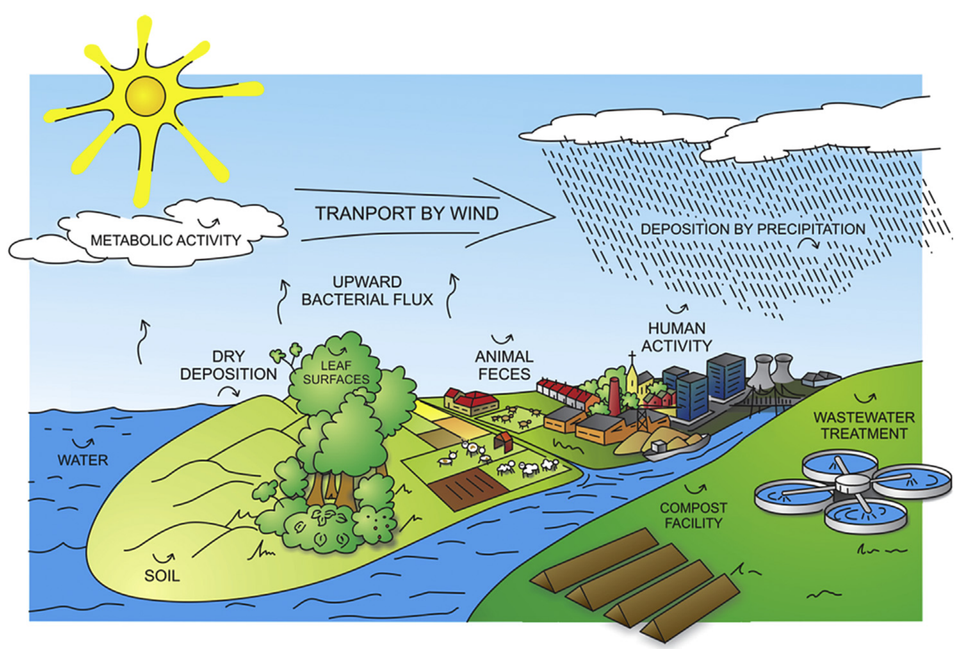

Fig. 1. Scheme of typical processes that determine the composition of local airborne bacterial communities. Abundant sources of aerosolized bacteria are marked with an upward arrow. Soil and leaf surfaces are often considered the main contributors of airborne bacteria (Bowers et al., 2011b). Other sources of airborne bacteria include water bodies (Blanchard, 1989; de Leeuw et al., 2011), humans and animals (Fujimura et al., 2010; Pan et al., 2003; Sciple et al., 1967; Zhao et al., 2014), faecal material (Bowers et al., 2011b), wastewater treatment (Han et al., 2012), and composting facilities (Albrecht et al., 2007). In case airborne bacteria are transported upwards, indicated as upward flux, they can be transported over medium or long distances and may occur in cloud droplets. Mechanisms leading to deposition are indicated with a downward arrow.