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Review

Bioaerosols in the atmosphere: A comprehensive review on detection methods, concentration and influencing factors

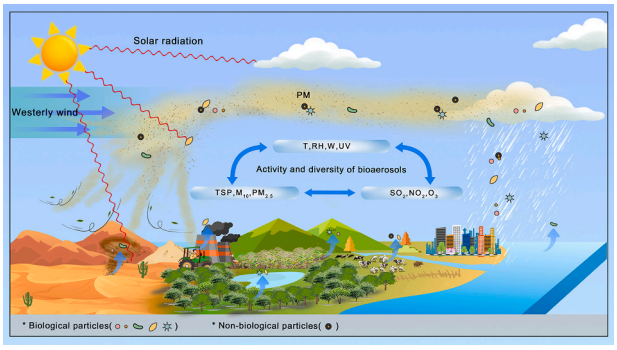
Zhongwei Huang [a,b], Xinrong Yu [a], Qiantao Liu [a], Teruya Maki [c], Khan Alam [d], Yongkai Wang [a], Fanli Xue [a], Shihan Tang [a], Pengyue Du [a], Qing Dong [a], Danfeng Wang [b], Jianping Huang [a,b,*]

[a] Key Laboratory for Semi-Arid Climate Change of the Ministry of Education, College of Atmospheric Sciences, Lanzhou University, Lanzhou 730000, China
[b] Collaborative Innovation Center for Western Ecological Safety, Lanzhou University, Lanzhou 730000, China
[c] Department of Life Science, Faculty of Science and Engineering, Kindai University, Higashiosaka, Osaka, Japan
[d] Department of Physics, University of Peshawar, Peshawar 25120, Pakistan

HIGHLIGHTS

- Systematic presentation of online and offline detection techniques for atmospheric bioaerosols.
- The emission and overall spatiotemporal distribution characteristics of bioaerosols were reviewed.
- The impact mechanism of atmospheric environment on bioaerosols is revealed.

GRAPHICAL ABSTRACT



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ABSTRACT

In the past few decades, especially since the outbreak of the coronavirus disease (COVID-19), the effects of atmospheric bioaerosols on human health, the environment, and climate have received great attention. To evaluate the impacts of bioaerosols quantitatively, it is crucial to determine the types of bioaerosols in the atmosphere and their spatial-temporal distribution. We provide a concise summary of the online and offline observation strategies employed by the global research community to sample and analyze atmospheric bioaerosols. In addition, the quantitative distribution of bioaerosols is described by considering the atmospheric bioaerosols concentrations at various time scales (daily and seasonal changes, for example), under various weather, and different underlying surfaces. Finally, a comprehensive summary of the reasons for the spatiotemporal distribution of bioaerosols is discussed, including differences in emission sources, the impact process of meteorological factors and environmental factors. This review of information on the latest research progress contributes to the emergence of further observation strategies that determine the quantitative dynamics of public health and ecological effects of bioaerosols.

* Corresponding author at: Key Laboratory for Semi-Arid Climate Change of the Ministry of Education, College of Atmospheric Sciences, Lanzhou University, Lanzhou 730000, China.
E-mail address: hjp@lzu.edu.cn (J. Huang).

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1. Introduction

Bioaerosols refer to living aerosol particles (e.g., bacteria, fungi, viruses, and other microbial particles), active particles (e.g., pollen, spores), and various plasmids released into the atmosphere by living organisms (Du, 2006). They are ubiquitous in natural environments and human living environments. Considering their properties of ordinary aerosols and biological characteristics, bioaerosols are crucial in health, climate and ecosystems.

Bioaerosols are a class of allergens and pathogens that affect the health of living organisms. They are dispersed through the air and enter the human body through the respiratory, digestive tracts, damaged skin and mucous membranes, which cause respiratory diseases, infectious diseases, and cancers (Hayleeyesus et al., 2015; Kim et al., 2018). The occurrence of these diseases may be facilitated when bioaerosols interact with air pollutants (Franze et al., 2005; Reid and Gamble, 2009). Allergic sensitization is enhanced when particulate matter (PM) acts as the carrier of bioaerosols (Ormstad et al., 1998; Parnia et al., 2002). Nitrification in polluted air significantly increases the sensitizing potency of allergens (Shiraiwa et al., 2012). The ravage of infectious diseases is often caused by the rapid spread of microorganisms in the air. In recent years, there has been a global epidemic of COVID-19 caused by the SARS-CoV-2 virus. When the virus exists in the aerosol form, it is prone to causing several acute respiratory problems (Morawska and Cao, 2020). As a result, the transport of virus-laden particles in the air has become a highly noticeable route of infection (Morawska and Cao, 2020; Mukherjee et al., 2021; Wang et al., 2021; Yao et al., 2020). Detection of airborne microorganisms has become a critical component in controlling epidemics. Widespread agricultural yield loss caused by airborne microorganisms is also concerning. Long-distance dispersal of fungal spores by wind can spread plant diseases across continents and reestablish diseases in areas where host plants are seasonally absent (Brown and Hovmøller, 2002). For instance, coffee leaf rust is a typical crop disease, and urediniospores on infected coffee leaves are easily picked up by the wind and spread among crops that are planted over large regions, causing devastating losses (Lucas et al., 1992). Notably, these plant diseases caused microorganisms can trigger a chain reaction and ultimately affect human health. Shelton et al. (2023) noted that the widespread use of the agricultural fungicide tebuconazole, which is effective in treating rusts on a wide range of crops, has caused the development of the azole-resistant variant of *Aspergillus fumigatus* (an opportunistic human fungal pathogen adapted for airborne dispersal) that has increased the probability of treatment failure in patients with Aspergillus disease.

Bioaerosols play an important role in global climate change by influencing physicochemical processes in the atmosphere. Bioaerosols absorb and diffuse solar radiation and thermal infrared longwave radiation, directly affecting regional and global radiative forcing (Gurton et al., 2001; Guyon et al., 2004; Spänkuch et al., 2000). Cell lysis and desorption of microorganisms during collision or contact can alter the chemical composition of atmospheric organic compounds and drive chemical reactions (including photochemical reactions) at environmental interfaces such as air/snow (Ariya and Amyot, 2004; Deguillaume et al., 2008). Microbe-driven chemical reactions in the atmosphere lead to changes in aerosol composition, which in turn affects the reactivity and balance of atmospheric species. These processes ultimately feed back into climate effects (Meinander et al., 2022). Furthermore, bioaerosols influence cloud and precipitation formation by acting as cloud condensation nuclei (CCN) and ice nuclei (IN) (Bauer et al., 2003; Haga et al., 2013). As a habitat for high-altitude microorganisms, clouds contain substances that support heterotrophic bacterial metabolism (Sattler et al., 2001; Womack et al., 2010). Microorganisms participate in the material cycle in clouds in various ways (mineralization, nitrification, etc.) (Hill et al., 2007), thus enabling their growth and reproduction in cloud droplets. Some special bioparticles have been detected in clouds, rain and snow (Amato et al., 2007a; DeLeon-Rodriguez et al., 2013; Morris et al., 2008). These biological aerosols can be activated to become CCN at relatively low supersaturation levels (Bauer et al., 2003; Pope, 2010) and trigger icing at higher temperatures (Hoose and Möhler, 2012). Bioaerosols' superior nucleation efficiency over abiotic particles is particularly relevant in cloud environments with temperatures above −15 °C (Morris et al., 2014). The contribution of bioaerosols to CCN or IN and precipitation regulation are particularly prominent in pristine atmospheric and local environments with less anthropogenic influence, such as vegetated areas, remote continents and oceans (Healy et al., 2014; Huffman et al., 2013; Lee et al., 2015; Pöschl et al., 2010; Prenni et al., 2009).

Bioaerosols are also important members of ecosystems. It is known that, as the earliest life on Earth, primitive microorganisms catalyze early environmental transformations and life evolution. After the emergence of primitive land, plants inherited the ability of cyanobacteria to photosynthesize and formed mutually beneficial symbioses with microbes to colonize the land. The evolution of such interactions has shaped diversity in ecosystems and continues to drive plant evolution today (Delaux and Schornack, 2021). Microbes carry the core metabolic machines (Falkowski et al., 2008) and are regarded as the engineers of ecosystems. Coban et al. (2022) noted that microbes can play the leading role in restoring degraded land, improving soil hydraulics (e.g., infiltration and water retention), and reducing soil hydrophobicity, which together contribute to ecosystem restoration. Entering the atmosphere for long-distance transport is an important survival strategy for many microorganisms (Gage et al., 1999). In this way, these microorganisms enter new habitats and affect local ecosystems. A typical example is the decline in coral reefs due to microorganism's invasion through dust (Garrison et al., 2003).

Previous reviews focused on summarizing the effects, molecular detection methods, sources and transport of atmospheric bioaerosols (Fröhlich-Nowoisky et al., 2016; G.S.J et al., 2023; Gollakota et al., 2021; Yoo et al., 2017). Little is known about the spatial-temporal characteristics and causes of changes in bioaerosols. We comprehensively introduce offline and online detection methods for atmospheric bioaerosols, spatiotemporal characteristics of concentrations, emission sources, and impact mechanisms of atmospheric environmental elements on bioaerosols. We then provide some future predictions of bioaerosols. Our work aims to provide a resource for future researchers by summarizing the latest achievements in bioaerosol research.

2. Bioaerosol detection methods

Bioaerosol detection techniques can be broken down into two distinct groups: offline and online method. The offline methods rely on manual sampling input and identification, whereas the online techniques detect atmospheric particles directly. Impactors, impingers, filters, cyclones, condensation-based samplers and electrostatic samplers are the major types of airborne bioaerosol samplers, as shown in Fig. 1. Cultivation methods, microscopy (e.g., fluorescence microscopy, scanning electron microscopy), molecular biological detection (e.g., polymerase chain reaction, DNA sequencing, chemical tracing), immunological detection, spectroscopy, and mass spectrometry are all examples of analytical techniques (An et al., 2023; Ghosh et al., 2015; Gollakota et al., 2021; Huffman et al., 2020; Yoo et al., 2017). Several frequently used methods are described in this work, which are illustrated with their basic operations as shown in Figs. 1 and 2. In addition, Table 1 provides a brief comparison of common techniques to identify bioaerosols.

2.1. Offline method

2.1.1. Sampling method

The sampling techniques for bioaerosols can be divided into two major categories: Passive and active methods (Manibusan and Mainelis, 2022; Sajjad et al., 2023). Passive samplers rely mostly on gravitational

deposition, electrostatic attraction, or their combination to deposit particles on the collection medium (Manibusan and Mainelis, 2022). Passive samplers are easy to use and are often used for qualitative studies. Exposing a petri dish to air for a period is a common passive sampling method. In contrast, active samplers require a pump or power source to draw air at a certain flow rate and collect the particles onto a medium (Manibusan and Mainelis, 2022). Mechanisms of collection include interception, impaction, diffusion, and electrostatic attraction. When sampling flow is low, diffusion is the main way to collect smaller particles in many active samplers (Delort and Amato, 2018). Active sampling is an advantageous means of obtaining quantitative bioaerosol data. We next describe active samplers commonly used in the collection of atmospheric bioaerosols (Fig. 1).

Impactors utilize the operating mechanism of inertial impact to

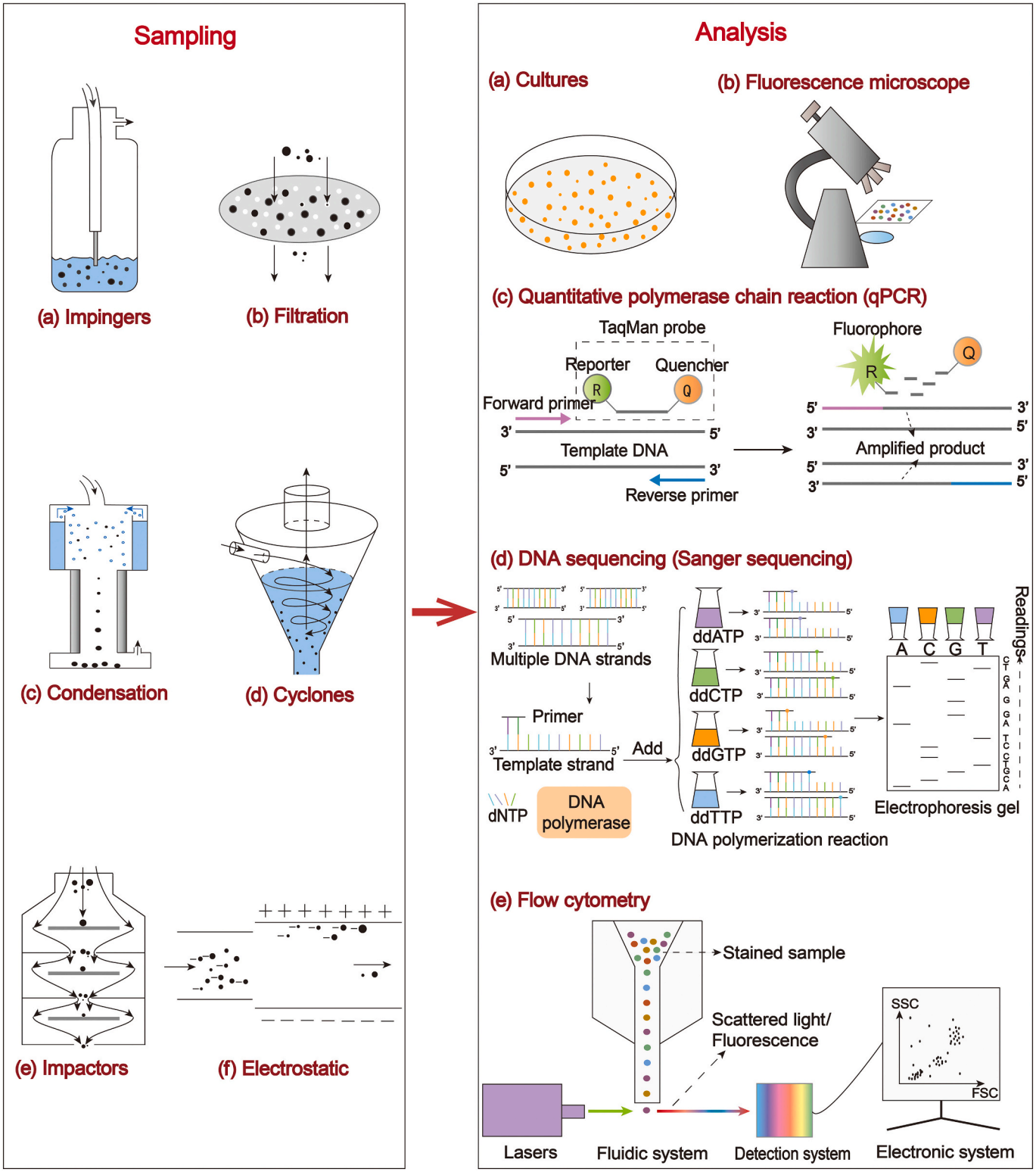

Fig. 1. Summary of offline methods for detecting bioaerosols. FSC: forward scatter. SSC: side scatters.

gather particles larger than a certain size that impact a solid surface. The Anderson sampler is a effective and widely used cascade impactor for collecting airborne microorganisms (Lundholm, 1982), with six particle size ranges of >7.0 μm, 4.7–7.0 μm, 3.3–4.7 μm, 2.1–3.3 μm, 1.1–2.1 μm and 0.65–1.1 μm. The most significant advantage of this sampler is the ability to collect multiple fixed-size samples simultaneously. Similarly, impingers use the principle of impact to collect particles. Nevertheless, the collection medium of impingers is liquid, the impact force is more moderate, and it is effective in preventing particles from drying out. However, both impactors and impingers have low collection efficiency for particles <500 nm (Pan et al., 2019). SKC BioSampler, All-Glass Impinger, and Multistage Liquid Impinger are common commercial impingers. Cyclones utilize air rotation to generate centrifugal force, which deflects particles from the airflow to impact the surface of the collection medium. Conventional cyclones are mainly used to collect large particles with high flow rates, and their efficiencies in collecting particles are slightly lower than those of impactors (Bhardwaj et al., 2021). Similar to the impingers and impactors, the damage to microbial viability in cyclone separators is mainly due to the high impaction forces. Filtration is a relatively simple and low-cost technology. Its collection mechanisms include interception, inertial impact, diffusion and electrostatic attraction (Bhardwaj et al., 2021). Particles in the air are collected on the filter medium as air flows through the pores. Filter materials (e.g., fiberglass, gelatin, polycarbonate, and Teflon) should be selected based on subsequent analysis. Filters have good collection efficiencies and perform excellently in sampling viruses. However, the dry environment during filter sampling tends to dehydrate and kill microorganisms. During the operation of a condensation-based sampler, air carrying microorganisms are first introduced into a warm and water-vapor-filled duct. Once the supersaturated air enters the cooling chamber, particles such as microorganisms serve as condensation nuclei and gradually form larger droplets. These droplets are eventually collected as gentle impacts on liquid/solid surfaces. This sampler can effectively collect small-sized microorganisms such as viruses. However, attention should be given to the impact of high temperatures generated during the operation of condensing samplers on microbial viability. Electrostatic samplers discharge to charge particles in the air. When these particles pass through an electric field, they fall to the collection surface due to electrostatic attraction. Notably, the discharge of electrostatic samplers and their electric field may destroy microbial activity, and ozone (a microbial inactivator) is produced during sampling. It is probably not suitable for studying bioaerosol viability, especially for infectious viruses (Pan et al., 2019). Electrostatic samplers' high collection efficiency for particles over a wide range of sizes, however, deserves recognition (Bhardwaj et al., 2021).

The choice of appropriate bioaerosol sampler depends mainly on the research objectives (Fahlgren et al., 2011; Haig et al., 2016). Researchers should consider the bioaerosol collection efficiency of the samplers and the effect of the operating principle of the samples on microbial viability (Haig et al., 2016). It should be noted that for all samplers, sampling flow is also an important factor affecting the collection efficiency and viability of bioaerosol (Delort and Amato, 2018; Rahmani et al., 2020). Large air flows cause loss of sample on the collection medium (usually membrane filters) and damage bacterial cells already collected on the medium (Zhang et al., 2017). Choosing appropriate values is challenging in studies involving microbial activity.

2.1.2. *Analysis method*

2.1.2.1. Cultivation. Cultivation is a traditional quantitative method. Specifically, microorganisms are cultured by collecting, plating onto solid or liquid media, incubating them at the appropriate temperature for a certain time to form visible colonies, and then counting the colonies (Fig. 1), so-called colony-forming-units (CFUs). Different bacteria require different liquid/solid media. In order to study the growth of various species or to restrict the growth of unrelated organisms, it is also feasible to blend media or insert additives into the medium (Delort and Amato, 2018). This culture-based approach can detect only viable and

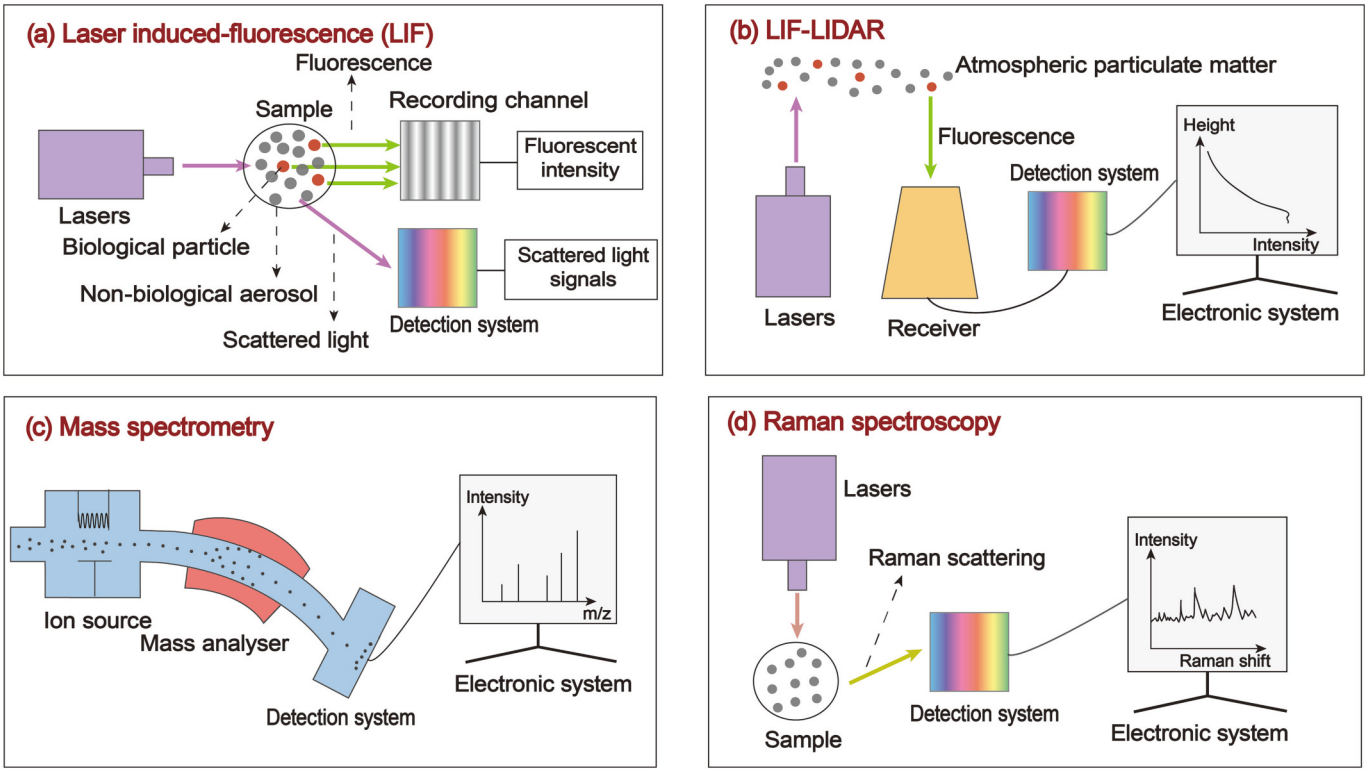

Fig. 2. Summary of online methods for detecting bioaerosols. (a) Laser-induced fluorescence (LIF). (b) Laser-induced fluorescence light detection and ranging (LIF lidar). (c) Mass spectrometry, *m/z*: mass-to-charge ratio. (d) Raman spectroscopy.

culturable microorganisms, while most microorganisms in the environment are often unculturable (Amann et al., 1995; Bridge and Spooner, 2001; Lewis et al., 2010; Peccia and Hernandez, 2006; Riesenfeld et al., 2004). Researchers have shown that approximately 17 % of fungi (Bridge and Spooner, 2001) and an average of <1 % of bacteria (Amann et al., 1995; Delort and Amato, 2018; Lewis, 2009) can grow in culture. The microbial culture rate is also significantly affected by the experimental settings (growth medium type, temperature, humidity, length of growth period, etc.) (Amato et al., 2007a; Després et al., 2012; Pillai and Ricke, 2002; Wang et al., 2008). In addition, there are cases of indistinguishable cell aggregation during counting, leading to multiple colonies being considered as one. This means that the culture-based colony counting method is not appropriate for determining the total level of microorganisms because it grossly underestimates the concentration of microorganisms in the environment. Nonetheless, it is still a mainstream method due to its cost-effectiveness and relevance in demonstrating the ability of microorganisms to survive and grow.

Table 1
Summary of current methods for detecting bioaerosols in the literature.

Category	Name	Detection principle	Measurement items	Advantages	Disadvantages	Ref
Offline	Culture medium	Colonies form on petri dishes	Number and community species of microorganisms	Effectively prove microbial activity Simple operation	It can only characterize viable and culturable microorganisms Culture conditions limit microbial growth	(Delort and Amato, 2018) (Palmgren et al., 1986) (Kepner Jr. and Pratt, 1994)
	Fluorescence microscope	Fluorescent staining	Number of viable/non-viable microorganisms	Simple operation Low cost	Particle identification is highly subjective	(Li and Huang, 2006) (Liu et al., 2023) (Lange et al., 1997)
	Flow cytometry	Light scattering Laser induced fluorescence	Forward light scatter Side light scatter Multiple fluorescent parameters	Fast Single cell detection A lot of information is provided	Abiotic particles of the same size as cells were counted Large error in cell aggregate counting High cost of equipment and human resources	(Chen and Li, 2005) (Adan et al., 2017) (Manohar et al., 2021)
	qPCR	DNA extraction, amplification and analysis	Fluorescence signal	The fluorescence changes during amplification are detected in real time and continuously Semi quantitative results can be provided Higher sensitivity and specificity Short detection time	DNA extraction procedures are complex Probe design is difficult and expensive Dyes can bind to nonspecific amplified DNA It cannot distinguish dead/living cells by itself	(Higuchi et al., 1992) (Kralik and Ricchi, 2017) (Harshitha and Arunraj, 2021) (Taylor et al., 2019) (Hugenholtz and Tyson, 2008)
	DNA sequencing	DNA extraction, amplification, sequencing	Community composition, diversity, metabolism	High sensitivity Accurate and reliable Numerous products	DNA extraction, sequencing process, and analysis of results all require a high level of skill	(Heather and Chain, 2016)
	UV-APS	Laser induced fluorescence	Particle size (aerodynamic diameter Da) Intrinsic particle fluorescence Particle side-scatter light intensity	Detect overall trends The total integration time can be defined by the operator (seconds to minutes)	No information of individual particle	(Hairston et al., 1997) (Healy et al., 2014) (Huffman et al., 2020) (Kaye et al., 2005)
	WIBS-4	Laser induced fluorescence	Particle size (optical diameter Do) Particle asymmetry(Af) Intrinsic particle fluorescence	Three channels (FL1, FL2, FL3) Smaller and lighter, easy to transport Record each particle	The repeatability between instruments is relatively poor	(Healy et al., 2014) (Huffman et al., 2020) (Christesen et al., 1994)
	LIF-LIDAR	Laser induced fluorescence	Total fluorescence	Long detection distance High spatiotemporal resolution	No sign of particles Quantization the concentration is complicated It was mainly used as a warning method Lack of information on some size biological particles	(Richardson et al., 2019) (Joshi et al., 2013) (Meuzelaar and Kistemaker, 1973)
	Mass spectrometry techniques	Mass analysis of charged ions	Mass charge ratio	Fast detection speed High sensitivity Rich detection types	Substances not in the library cannot be identified The overlapping of spectra is challenging to analyze	(Krásný et al., 2013) (Jarvis and Goodacre, 2008)
	Raman spectra	Raman scattering	Raman scattering intensity	Fast Non-invasive High specificity	Data analysis is cumbersome and complex Spectral database needs to be improved	(Ashton et al., 2011) (Pahlow et al., 2015)

2.1.2.2. Staining-fluorescence microscopy. Fluorescence microscope is a commonly used instrument for measuring the total number of atmospheric microorganisms (unit: cells m^{-3}) (Després et al., 2012; Kepner Jr. and Pratt, 1994; Maki et al., 2013; Palmgren et al., 1986). Microbes are detected and counted using fluorescence microscopy by labeling samples with specialized fluorescent dyes and then analyzing them for characteristics like particle luminous color and particle size (e.g., Fig. 1). The main stains commonly used in aerobiology include DAPI (4′, 6-diamidino-2-phenylindole), SYBR® Green I and II, SYBR® Gold, SYBR® Safe, Live/Dead® (BacLigh™), CTC (5-cyano-2,3-diphenyl tetrazolium chloride) and Acridine Orange (AO) (Delort and Amato, 2018; Li and Huang, 2006). DAPI and Live/Dead® (BacLight™) are the most used stains for determining the concentration of airborne microorganisms. The specific operation can be found in the literature (Hara et al., 2011; Li et al., 2011; Liu et al., 2023; Murata and Zhang, 2013). DAPI is applied to determine the total number of microorganisms including bacteria, archaea and unicellular eukaryotes (Mayol et al., 2014). Live/Dead® (BacLight™) can be used to quantify live and dead bacteria and is composed of two stains that can combine with DNA, SYTO 9 and PI. When compared to PI, which can pass through only damaged cell membranes, SYTO 9 can pass through both intact and damaged membranes (alive and dead cells). After treatment of samples with this stain, green or red spherical spots (diameter close to or <1 μm) are considered as bacterial cells in the field of fluorescence microscope with ultraviolet light (Hara and Zhang, 2012; Murata and Zhang, 2014). Manual sorting and counting under a microscope introduce a substantial human factor and computational burden. Therefore, it is gradually used in combination with computer-based automated systems for image analysis (Carrera et al., 2005; Ghosh et al., 2015; Kildesø and Nielsen, 1997). Counting the number of microorganisms in the air using this method is considered reliable.

2.1.2.3. Flow cytometry. Flow cytometry (FCM) is a powerful instrument based on the principles of light scattering and fluorescence emission. This instrument can be used for cell counting, characterization and sorting. Its structure and detailed principle were described in previous studies (Adan et al., 2017; Manohar et al., 2021). The principle of FCM is shown in Fig. 1. Flow cytometers work by passing a laser beam through the solution containing suspended particles and simultaneously measuring several characteristics of those particles, including their fluorescence, forward and backward light scattering. Then, the particles are studied further using the correlation between light scattering and cell structure and morphology, as well as the correlation between the number of fluorescent probes bound to a cell or cellular assembly and the intensity of the probe′s fluorescence emission (Adan et al., 2017; Macey, 2007). Thus, the numerical concentration of microorganisms (cells mL^{-1}) is obtained. In practice, FCM is often combined with fluorescent dyes (Chen and Li, 2005; Lange et al., 1997; Liang et al., 2013), imaging techniques (Han et al., 2016), microfluidics (Gong et al., 2018; Piyasena and Graves, 2014), etc., to achieve analytical purposes. Among them, the combination with fluorescence techniques (FCM/FL) is a widely used technique for rapid and accurate determination of total microbial concentration. FCM analysis can use the same fluorescent dyes as fluorescence microscopy to distinguish cells and nonbiological particles. FCM equipment has been used by researchers to measure atmospheric microbial concentrations (Bowers et al., 2012). FCM can count thousands of cells in a second and tens of thousands of particles in a second in a nondestructive manner (Chen and Li, 2005; Davey and Kell, 1996; Han et al., 2016; Liang et al., 2013), which facilitates the processing of large numbers of samples. However, FCM equipment is cumbersome, expensive, and requires specialized operational skills. FCM is notable for its ability to detect individual cells. However, it has significant drawbacks when trying to identify microbes that congregate.

2.1.2.4. Quantitative polymerase chain reaction (qPCR). Molecular biological detection methods are widely utilized for bioaerosol characterization (Blais-Lecours et al., 2015; Yoo et al., 2017). Quantitative polymerase chain reaction (qPCR) is regarded as a representative method that can better reflect the concentration of specific microorganisms in environmental samples (Harshitha and Arunraj, 2021; Lee et al., 2010; Li et al., 2021; Taylor et al., 2019). This method monitors DNA amplification in real time by fluorescence (Higuchi et al., 1992; Holland et al., 1991; Kralik and Ricchi, 2017) (Fig. 1). Quantification is realized by using the linear relationship between the starting template amount and the logarithm of the PCR product amount in the exponential growth period of the fluorescence signal. The microorganism cell concentration in the air is expressed by the number of gene copies per cubic meter of air (copies m^{-3}) (Tignat-Perrier et al., 2020). SYBR Green I fluorescent dyes and TaqMan probes are frequently employed to generate fluorescent signals. The SYBR Green I fluorescent dye has a low fluorescence intensity when free, but a large enhancement when combined with double-stranded DNA. The TaqMan probe will be cut off during DNA strand formation to form fluorescent molecules. There is a direct correlation between the amount of DNA amplification, the number of fluorescent molecules, and the number of cut probes. This method enables real-time continuous detection of fluorescence changes during amplification. It can provide semiquantitative results (i.e., ploidy above/below reference material) in the absence of standards but with reference material (Kralik and Ricchi, 2017). Although the qPCR technique has high specificity and sensitivity and can significantly reduce testing time, the complexity of the DNA extraction procedure requires expert skill, and the design knowledge of primers and fluorescent probes is also needed. Fluorescent dyes bind to both specific and nonspecific double-stranded DNA (Harshitha and Arunraj, 2021), which may produce false positive signals. In addition, qPCR cannot distinguish between live and dead cells (Kralik and Ricchi, 2017).

2.1.2.5. DNA sequencing. Species can be identified by comparing the sequences obtained from amplified DNA fragments with those already present in databases. The properties, species, and composition of bioaerosols can be studied with the help of DNA sequencing. A British biochemist named Frederick Sanger invented the original Sanger sequencing method in 1997. The method requires four kinds of dideoxynucleotide triphosphates (ddNTPs) to terminate DNA synthesis. DNA polymerization can produce several new DNA strands of varying lengths due to the random nature of ddNTP binding. Next, gel or capillary electrophoresis is used to obtain sequencing data (e.g., Fig. 1). Its major drawbacks are the high cost and relatively short length of a single measured sequence, making it challenging to keep up with the current demand for genetic data. With the rapid development of next-generation sequencing technology (NGS, also known as high-throughput sequencing), various NGS platforms and technologies for environmental DNA have emerged (Heather and Chain, 2016; Mardis, 2013; Shokralla et al., 2012). High-throughput sequencing based on rRNA genes and ITS (internal transcribed spacer) regions is a suitable method to study microbial community information (taxonomic composition, community diversity, evolutionary relationships among taxonomic categories) (Maki et al., 2017; Qi et al., 2021; Qi et al., 2022a; Tang et al., 2018). Metagenomic analysis using shotgun sequencing, which can further provide a reference for microbial functional composition and metabolic activities, is a challenging and promising new tool (Hugenholtz and Tyson, 2008). Currently, many biological companies provide paid sequencing services. Researchers can directly utilize the obtained operational taxonomic unit (OTU) data for microbial species identification, which makes the use of DNA sequencing more convenient and common. However, acquiring a high-quality template from a complex DNA extraction process necessitates a high level of expertise, and PCR amplification may cause taxonomic biases and artifact nucleotides. Additionally, matching sequencing result requires a large database that is continuously updated.

2.2. Online method

2.2.1. Laser-induced fluorescence (LIF)

The most popular method of real-time bioaerosol detection is laser-induced fluorescence (LIF), which has greatly improved the temporal and spatial resolutions of bioaerosol concentration data. LIF instruments mainly detect the fluorescence signals of riboflavin, nicotinamide adenine dinucleotide (NADH, the bacterial metabolite) and common amino acids (such as tryptophan, phenylalanine, tyrosine) in biomolecules (Eversole et al., 2001; Hairston et al., 1997; Ho, 2002; Huffman et al., 2020; Pinnick et al., 1995). Fig. 2a displays a real-time characterization of bioaerosols based on the fluorescence emission intensity of individual particles at the characteristic wavelength of the biofluorophores following pulsed excitation (O'Connor et al., 2011; Pöhlker et al., 2013; Pöhlker et al., 2012). A combination of different excitation and emission bands enables the detection of different biofluorophores. Instruments for detecting bioaerosols using LIF methods have been extensively developed in recent years. The Wideband Integrated Bioaerosol Sensor (WIBS) and Ultraviolet Aerodynamic Particle Sizer (UV-APS) are two of the most widely used commercially available optical system instruments for civilian use (Fennelly et al., 2018; Hairston et al., 1997; Healy et al., 2014; Huffman et al., 2020; Kaye et al., 2005; Könemann et al., 2019). They provide number concentrations per cubic meter (counts m-3), which is similar to instruments for detecting ordinary atmospheric particulate matter.

Individual particles are excited by UV pulses from a xenon lamp (280 nm and 370 nm), with the resulting 310–400 nm and 420–650 nm fluorescence emission bands recorded by the Wideband Integrated Bioaerosol Sensor (WIBS-4). Therefore, it provides three fluorescence detection channels for each particle (FL1: 280 nm excitation and 310–400 nm recording; FL2: 280 nm excitation and 420–650 nm recording; FL3: 370 nm excitation and 420–650 nm recording). Both the FL1 and FL2 channels, excited by 280 nm light, can detect proteins, amino acids, and other biofluorophores. However, the difference between the two channels highlights different molecules. Pöhlker et al. (2012) demonstrated that the FL1 channel is more efficient in detecting certain amino acids and proteins, while the FL2 channel is more efficient in detecting flavin compounds (natural pigments, including riboflavin). With a smaller volume and lighter weight than UV-APS, WIBS-4 is easy to transport and deploy in the field. The instruments in the WIBS series have been utilized in alpine areas, tropical rainforests, urban areas, rural areas, polar areas and other regions (Crawford et al., 2017; Crawford et al., 2016; Gabey et al., 2011; Ma et al., 2019; Moallemi et al., 2021; Toprak and Schnaiter, 2013). The main advantages of this instrument are the recording of each particle, the ability to analyze very low particle concentrations and the ability to analyze almost any desired time scale (Delort and Amato, 2018). However, WIBS instruments are not always repeatable due to differences in operational parameters (Healy et al., 2014; Huffman et al., 2020).

UV-APS emits 355 nm light from a Nd:YAG laser to excite fluorescence signals. The fluorescence emission of particles is detected in the 420–575 nm wavelength range. Within a time frame (seconds to minutes) set by the user, it reports the total number of particles, their fluorescence intensity, and size. Nevertheless, UV-APS cannot spectrally resolve the fluorescence emission. It does not provide information on individual particles. In comparison to multi-channel equipment, it provides worse single-channel fluorescence data. Besides, the ability of UV-APS to detect biological particles, such as damaged cells, is limited. Without data analysis tools, it is challenging to comprehend complicated data sets in detail. The aforementioned drawbacks are summarized in the cited works (Agranovski et al., 2004; Delort and Amato, 2018; Healy et al., 2014; Huffman et al., 2020; Huffman et al., 2012). Fluorescent particle concentrations measured by FL3 in WIBS have a high correlation with those measured by UV-APS because of their close excitation wavelengths (370 nm and 355 nm). The relative proximity of excitation wavelengths allows these channels to excite similar fluorophores in the particles (Gosselin et al., 2016; Healy et al., 2014). Healy et al. (2014) found a strong correlation between the fluorescent bioparticle concentration of UV-APS and fungal spores. This indicates its excellent performance in measuring fungal spores.

Many factors contribute to the uncertainty of LIF instruments: (1) difficulties in species-level identification because fluorescence spectra of bioaerosols are similar (Huffman et al., 2020); (2) incorrect identification of nonbiological particles that fluoresce as biological particles, which include secondary organic aerosols and those containing polycyclic aromatic hydrocarbon (PAH) components (e.g., soot particles from combustion processes) (Huffman et al., 2010; Lee et al., 2013; Pöhlker et al., 2012; Schauer et al., 2004); (3) the fluorescence of some bioaerosols is too weak to be detected (Healy et al., 2014); (4) particle concentrations larger or smaller than the set threshold are underestimated (Gabey et al., 2010; Healy et al., 2014); (5) instrument errors complicate the crossover between biological classification of particles and detection strategies (Schumacher et al., 2013); (6) laser-induced fluorescence spectra of PBAPs are significantly impacted by growth conditions, the interaction between biological particles and the growth medium, UV and ozone (Delort and Amato, 2018; Huffman et al., 2020; Pan et al., 2014a; Pan et al., 2014b; Sivaprakasam et al., 2011). Despite these uncertainties, the concentration of fluorescent aerosols detected by real-time instruments such as WIBS and UV-APS is considered the lower limit of PBAP (Huffman et al., 2010; Toprak and Schnaiter, 2013).

2.2.2. Laser-induced fluorescence lidar (LIF lidar)

Aerosols may be detected in real-time, with great spatial resolution, and across vast distances using lidar techniques (e.g., over ten kilometers). Regarding bioaerosol detection, LIF lidar is more effective and was developed earlier (Christesen et al., 1994; Gelbwachs and Birnbaum, 1973; Sugimoto et al., 2012). It usually uses high-power UV lasers with excitation wavelengths of 266 nm or 355 nm (e.g., by Nd: YAG lasers) to obtain fluorescence spectra in the detection range, as shown in Fig. 2b. The fluorescence excited by 266 nm radiation for LIF lidar is mainly from tryptophan, and 355 nm radiation is mainly from NADH (Pan, 2015; Richardson et al., 2019). The detection range of 266 nm light is highly limited (often <1 km) (Papayannis et al., 1990), because its atmospheric attenuation (primarily ozone absorption) is approximately 10 times higher than that of 355 nm light (Gorshelev et al., 2014). LIF lidar records only the total fluorescence intensity of diverse bioaerosol components without particle characterization. It difficult to quantify bioaerosol concentrations, distinguish bioparticle types, and determine each type's relative contribution to the total signal. Additionally, remote sensing detection suffers from the limitations of laser-induced fluorescence technology itself. Therefore, LIF lidar is primarily utilized as a qualitative means of warning biological warfare agents (Joshi et al., 2013). In an effort to enhance LIF lidar's detection capabilities, some researchers have focused on creating lidars that are superior in identifying a certain type of bioaerosol (e.g., Rao et al., 2017; Richardson et al., 2019; Saito et al., 2018). We have developed a novel fluorescence-meter lidar system for measuring fluorescent aerosols within the boundary layer (Wang et al., 2023). This new lidar system is capable of simultaneously collecting 32-channel fluorescence spectra, as well as backscattered signals and declination ratios in two bands (532 nm and 355 nm). It has the potential for real-time monitoring of fluorescent aerosols in the atmosphere due to its ability to detect the fluorescence signal of weak aerosol layers and obtain the fluorescence spectra and spatiotemporal distribution of fluorescent particles in varied weather situations. Lidar systems that rely on fluorescence might benefit considerably from employing several excitation wavelengths, creating a database of fluorescence spectra for various bioaerosols, and integrating offline processing.

2.2.3. Mass spectrometry

By analyzing the mass-to-charge ratio of ionized samples, mass spectrometry methods provide information on the material composition

of individual particles (e.g., Fig. 2c). A variety of mass spectrometry techniques and their coupling techniques have been successfully applied in bioaerosol detection, such as matrix-assisted laser desorption/ionization (MALDI) mass spectrometry and pyrolysis-gas chromatography–mass spectrometry (Py-GC–MS) (Creamean et al., 2013; Huffman et al., 2020; Jeong et al., 2014; Krásný et al., 2013; Meuzelaar and Kistemaker, 1973; Schneider et al., 2011; Shu et al., 2012; Simmonds et al., 1969; Steele et al., 2003). Markers are often chosen to substitute for the microorganism being studied in mass spectrometry. Proteins, carbohydrates, and lipids are only some of the typical biomarkers utilized in aerosol identification and classification. The strengths mass spectrometry are its quickness, sensitivity, and abundance of detection options. However, real-time mass spectrometers typically do not collect data on certain crucial bioaerosol particle sizes. Because such instruments have difficulty collecting particles >1 μm and only a small fraction of super-micron particles are ionized, most biological particles are larger than this size range (Delort and Amato, 2018). Mass spectrometry can be tricky because of overlapping spectra and chemicals that are not in the spectral library. Mass spectral patterns are affected by changes in laser power during the vaporization/ionization process (Steele et al., 2003; Wolf et al., 2017), which interferes with the measurements.

2.2.4. Raman spectroscopy

In many cases, the differences in Raman spectral intensities (e.g., Fig. 1) can also be used to identify bioaerosols (e.g., Fig. 2d) (Ashton et al., 2011; Ho et al., 2019; Kano and Hamaguchi, 2006; Laucks et al., 2000; Pahlow et al., 2015; Ronningen et al., 2014). Particularly, with the development of enhancement techniques that address the issue of weak intrinsic Raman signals, such as surface-enhanced Raman scattering (SERS), ultraviolet resonance Raman (UVRR), and tip-enhanced Raman (TERS), the application of Raman spectroscopy in microbiology has become more promising. SERS helps with the detection of low concentrations and is especially well suited for the investigation of single microorganisms (Jarvis and Goodacre, 2008; Rösch et al., 2006). Several researchers have successfully applied this technique for screening of the SARS-CoV-2 virus and obtained good results (Leong et al., 2022). Commercial Raman microscopy has developed into a crucial technique for identifying bioaerosols (especially microorganisms) (Huang et al., 2010). The Raman spectroscopy technique is characterized performing single-cell measurements, fast signal acquisition and high specificity, without destroying the sample during detection. However, as with other spectroscopic methods, Raman spectroscopy data analysis is tedious and complex. Moreover, the database of bioaerosol Raman spectroscopy needs further improvement.

3. Distribution of bioaerosol concentrations

Bioaerosol is an important component of atmospheric particulate matter. Overall, approximately 5 % of PM_{10} mass, which can reach up to 35 % in tropical rainforest environments, is made up of fungal spores (Elbert et al., 2007; Fröhlich-Nowoisky et al., 2009; Huffman et al., 2012). Total bioparticles such as fungal spores, pollen, and plant debris can contribute >10 % of the PM_{10} mass. The contribution is higher during the rainy season (Gosselin et al., 2016; Rathnayake et al., 2017), summer (Bauer et al., 2008; Perrino and Marcovecchio, 2016; Zhu et al., 2015), areas with strong agricultural activities (Bauer et al., 2008; Chow et al., 2015), forests (Gosselin et al., 2016; Huffman et al., 2012). In terms of quantity, the contribution of bacteria and total biogenic particles to particulate matter may be significantly lower in marine air than on continents (Hu et al., 2017; Matthias-Maser et al., 1999; Matthias-Maser et al., 2000a; Mayol et al., 2017). The contribution of bioaerosols is higher in vegetation-covered areas such as tropical rainforests and lower in permanently snowy mountain regions (Bowers et al., 2012; Gabey et al., 2010; Matthias-Maser et al., 2000b).

3.1. Seasonal variation of bioaerosols

There is a significant seasonal change in microorganisms' concentrations. Yet seasonal trends may not be consistent across the region (Fig. 3a, b), and sampling at different periods within the same region can yield different results (Fig. 3a). Previous studies have found that in the summer and winter seasons with the highest climate contrast, the comparison results of microbial concentrations in different regions may also be completely opposite. Observations in Qingdao by Li et al. (2011) showed higher microbial concentrations in summer and lower microbial concentrations in winter (left column of Fig. 3a). Similar trends were observed in Washington (Jones and Cookson, 1983), Beijing (Fang et al., 2005; Fang et al., 2007; Gao et al., 2014), Dublin (O'Gorman and Fuller, 2008), Milan (Bertolini et al., 2013), Sweden (Bovallius et al., 1978), Tijuana (Hurtado et al., 2014), Detroit and Cleveland (USA) (Bowers et al., 2011b). In contrast, the microbial concentrations at some sampling sites were lower in the summer and higher in the winter (Dong et al., 2016; Fahlgren et al., 2011; Haas et al., 2013; Xie et al., 2018b; Xu et al., 2011).

The obvious seasonal pattern has been captured by fluorescent biological aerosol particles (FBAPs) concentrations measured by online instruments such as WIBS and UV-APS. Concentrations were higher in the warmer months, peaked in the summer and dropped in the winter, as shown in Fig. 3c (Healy et al., 2014; Schumacher et al., 2013; Toprak and Schnaiter, 2013). Similar to the life cycle of plants (such as flowering and dormancy). The inhibition of spore release and floating ability by the snow barrier is a major factor influencing the decrease in concentrations during the cold season. Recently, Sjögren et al. (2023) found the highest FBAPs during the summer and lower FBAPs in winter at rural, forested site in Sweden. The FBAPs in Sweden exhibited 5 to 8

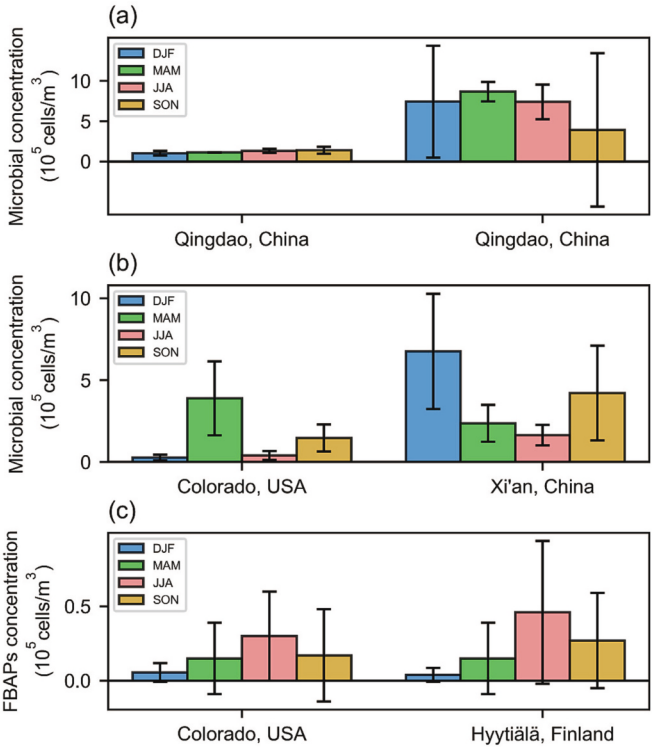

Fig. 3. Examples of the seasonal distribution of bioaerosol concentrations in the atmosphere. (a) Microbial concentrations at different sampling times in Qingdao, left column sampling time range 2009.7–2010.6 (Li et al., 2011), and right column 2016.9–2017.7 (Gong et al., 2019). (b) Microbial concentrations in Colorado, USA (Bowers et al., 2012) and Xi'an, China (Xie et al., 2018b). (c) FBAPs concentrations in Colorado, USA and Hyytiala, Finland (Schumacher et al., 2013).

folds difference between summer and winter.

It should be noted that some of the differences in seasonal results may also be caused by special weather events that occurred during sampling. The results of Yin et al. (2021) showed that seasonal variations in total airborne microbes concentration on non-special days (i.e., excluding dust, fog, haze-fog mixture, and haze days) were different from those for the total sampling days. Special days (fog, haze, haze-fog mixture, and dust days) increased total airborne microbes concentrations by 11 %, 91 %, and 36 % in spring, autumn, and winter, respectively, while they had less effect on microbial concentrations in summer.

3.2. Diurnal variation of bioaerosols

Microbial concentrations also showed significant diurnal changes. In October 2021, the bacteria were sampled at the Yuzhong County Observatory (located on a hilltop with sparse vegetation) in Lanzhou, China. The airborne bacterial concentrations ranged from high to low in the order of morning > afternoon > noon, with the lowest value of 1.58×10^5 cells/m^3 occurring at 13:00. The overall change was contrary to the variation in solar radiation intensity. Other research also reported the highest average microbial concentrations in the morning, followed by the afternoon, and the lowest variation at noon (Liu et al., 2008). Another study by Yang et al. (2021) conducted bioaerosol sampling at three different times (8:30, 18:00 and 21:30), and the results revealed that the airborne bacterial concentrations were highest at 8:30 and lowest at 18:00. They attributed such contrasting distribution to the thermal effect of the sun.

FBAPs concentrations showed a more consistent daily pattern. Cheng et al. (2020) showed two peaks of fluorescent bioparticles at sunrise (~7:00) and in the evening (~20:00). Toprak and Schnaiter (2013) indicated that FBAPs concentrations were higher at night and lower during the day, starting to decrease before sunrise and increasing after sunset, with the lowest values occurring at 12–3 PM. FBAPs in the Nanjing industrial area reached the lowest concentrations at noon and the highest concentrations around 3 AM to 6 AM. And the concentrations decreased rapidly after sunrise (Ma et al., 2019). Similar variations in FBAPs concentrations were also observed in other studies (Calvo et al., 2018; Cheng et al., 2020; Huffman et al., 2012; Ma et al., 2019; Ren et al., 2017). The magnitude of bioaerosol variation within a day is closely related to the season (Toprak and Schnaiter, 2013). A recent study by Huffman et al. (2012) suggested that the daily pattern of FBAPs is mainly caused by the combination of two mechanisms. First, the emission and dispersion of bioaerosols are closely related to environmental variables, which have a strong daily cycle. Second, the atmospheric boundary layer is thin at night. As the sun rises, turbulence and layer thickness are enhanced, and particles are brought to higher altitudes; thus, bioaerosol concentrations are diluted and reduced at the ground surface.

3.3. Variation of bioaerosols under special events

Special weather events (e.g., sandstorms, fog and haze) can cause noticeable variations in microbial concentration compared to sunny days. Microbial concentrations during dusty days were much higher than those on non-dusty days (Griffin et al., 2007; Tang et al., 2018; Wu et al., 2004). In dusty weather, microbial concentrations in Beijing and Japan were one to two orders of magnitude higher than those before the arrival of dust (Hara and Zhang, 2012; Yuan et al., 2017). The microbial concentrations in Seoul were seven times higher than those in normal weather (Jeon et al., 2011). Total microorganisms in Qingdao increased by 118.6 % after dust (Li et al., 2011). Across Qingdao, the Yellow Sea, and the Bohai Sea, the number of microbes increased by a factor of 1.6 to 49 after a dust event (Qi et al., 2022b) (Fig. 4b). The conclusion that dust events cause a higher concentration of bioaerosols is confirmed by four examples of the fluorescent aerosols vertical structure in the atmosphere that we observed using a fluorescent lidar in Linze (39.05 N, 100.12 E), China during April 2014, as shown in Fig. 5 (Wang et al., 2023). Fluorescent spectral between 420 and 510 nm was detected by a 32-ch spectrometer after excitation at 355 nm laser wavelength. The results demonstrate that there is a small amount of anthropogenic pollutants in the background aerosol at about 300–600 m, which produces a certain fluorescence reaction with a strength of <0.4. The overall fluorescence of air pollutant was quite high, with readings as high as 0.5 for the course of the measurements. The fluorescence signal of pure dust was weak (0.26). The polluted dust layer had a high fluorescence signal, which confirms that the dust bridged high concentrations of bioaerosols. Under weather conditions such as anticyclones and cold fronts, the microbes also vary obviously (Murata and Zhang, 2013). The foggy environment was favorable for microbial growth, and the microbial concentrations increased (Dong et al., 2016; Fuzzi et al., 1997; Li et al., 2017; Xie et al., 2018b). A comparison of microbial concentrations between hazy and non-hazy days showed two opposite results. Some results indicate that hazy days have much greater air microbial concentrations than non-hazy days (Dong et al., 2016; Li et al., 2015; Wei et al., 2016; Xie et al., 2018b). For example, Li et al. (2015) observed a 2–4-fold and 4–7-fold increase in bacterial and fungal concentrations, respectively, on hazy days compared to normal conditions in Xi′an. In contrast, some studies in Beijing showed a decrease in air microbial concentrations because of the unfavorable factors of haze days (Gao et al., 2015; Hu et al., 2015). Xie et al. (2018b) comprehensively studied the air microorganisms at different air quality levels (Fig. 6). The mean concentration varied in the following ascending order: Excellent ($1.92 \times 10^5 \pm 0.88 \times 10^5$ cells/m^3) < good ($2.39 \times 10^5 \pm 1.47 \times 10^5$ cells/m^3) < lightly polluted ($5.38 \times 10^5 \pm 3.26 \times 10^5$ cells/m^3) < heavily polluted ($5.93 \times 10^5 \pm 3.45 \times 10^5$ cells/m^3) < severely polluted ($7.23 \times 10^5 \pm 3.49 \times 10^5$ cells/m^3) < moderately polluted ($7.38 \times 10^5 \pm 4.43 \times 10^5$ cells/m^3). Precipitation events also significantly change atmospheric bioaerosol concentrations. The measurement data of fungi and bacteria measured in Seoul showed that bioaerosol concentrations during rain events were approximately seven times higher than those under non-rainy conditions (Heo et al., 2014). Schumacher et al. (2013) also observed a significant increase in the concentration of fluorescent particles due to rainfall. However, Li et al. (2017) reported that the lowest concentration of live microorganisms in the air was observed during rainy days. Obviously, the mechanisms of change during special weather are complex. Meteorological and environmental factors also contribute significantly to bioaerosol changes during special weather. We summarized these mechanisms of action in Section 4.

3.4. Variations of bioaerosols for different underlying surfaces

Bioaerosol concentrations vary significantly between regions. Overall, airborne microbial bacterial concentrations were typically in the range of 10^5–10^6 cells m^{-3} in terrestrial areas (Bowers et al., 2011a), 10^4–10^5 cells m^{-3} over the oceans (Hu et al., 2017; Qi et al., 2022b), and 10^6–10^7 particles m^{-3} in the desert (Maki et al., 2019). Bioaerosol concentrations were high in forest ecosystems and higher during rainfall (Echalar et al., 1998; Huffman et al., 2013; Huffman et al., 2012). Microbial concentrations in urban environments tend to be higher than those in the countryside (Dong et al., 2016; Harrison et al., 2005; Li and Huang, 2006; Yuan et al., 2017). Microbial concentration levels over different land use types (e.g., forest, wetland, lake, bare soil, cropland, wastewater treatment facility, street, livestock farm, smeltery, and garden) varied significantly, with land types heavily impacted by human activities (e.g., farmland, wastewater treatment plants, street smelters) likely to show higher microbial levels and lower cultivability (Li et al., 2020) (Fig. 7). Microbial concentrations over the ocean were generally lower than those over land. The main factors are the single source of the ocean and the short residence time of microorganisms over the ocean (Burrows et al., 2009a). Some measurements by Prospero et al. (2005) suggested that bacterial concentrations in the oceans could be 100–1000 times lower than those in the continental air. Microbial concentrations

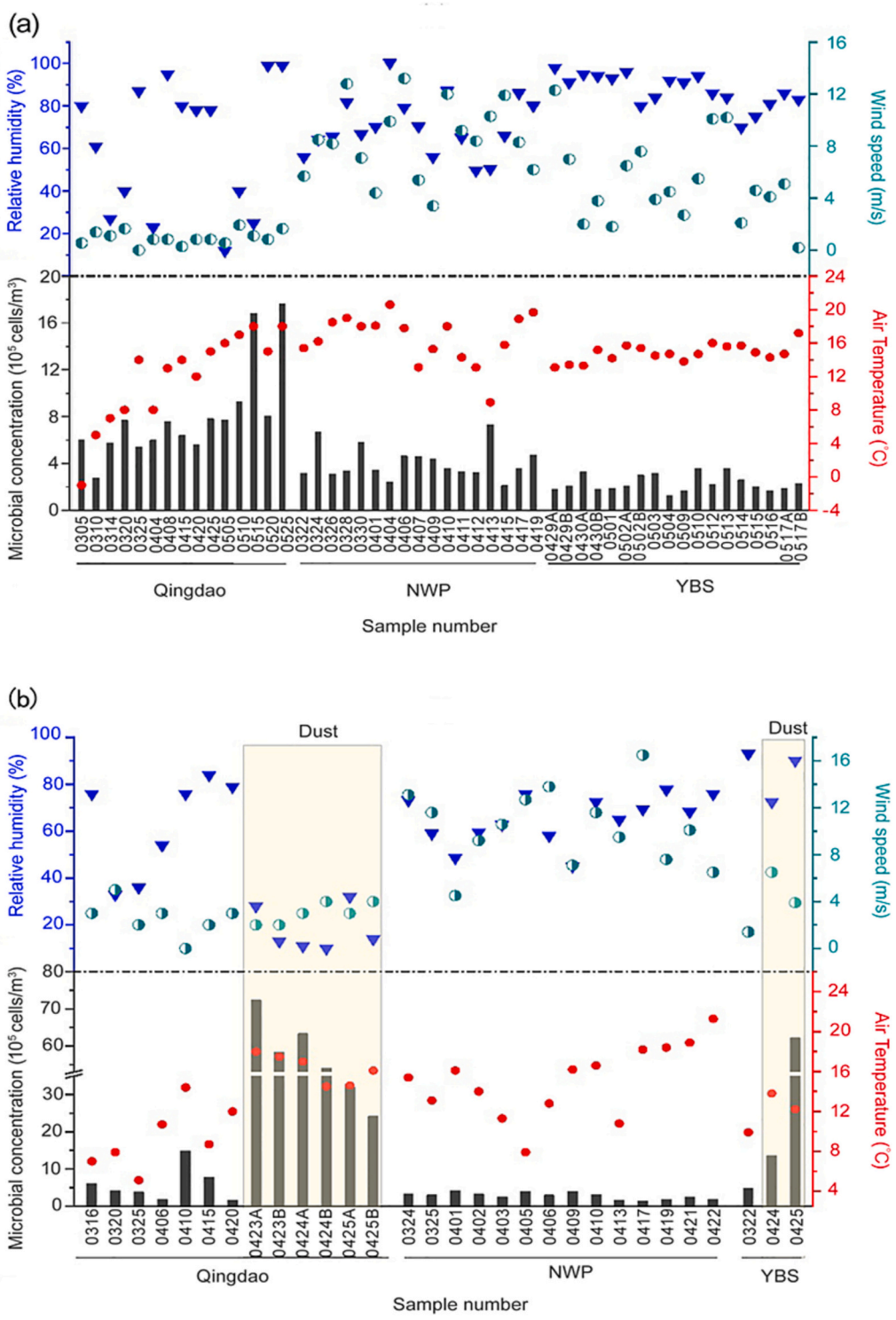

Fig. 4. The concentrations of the total airborne microbes over the Northwest Pacific Ocean (NWPO), the Yellow and Bohai Seas (YBS) and Qingdao (QD) in 2014 (a) and 2016 (b). From Qi et al. (2022b).

measured in the coastal city of Qingdao (Qi et al., 2022b) were significantly higher than those detected in the Yellow and Bohai Seas and the Northwest Pacific Ocean during the same period (Fig. 4). Moreover, there were multiplicative differences in microbial concentrations between different sea areas (Hu et al., 2017; Qi et al., 2022b). There are also differences in microbes between inland and coastal cities. Microorganisms in coastal areas are not only of terrestrial origin but can also be generated by the breaking of marine bubbles and waves. During 2016–2017, Gong et al. (2019) and Dong et al. (2016) conducted one-year sampling in a Chinese coastal city (Qingdao) and inland city (Xi'an), respectively. The results of these studies showed that the average concentration of total microorganisms in Qingdao was 6.84 × 10^5 cells m^{-3}, which was higher than that in Xi′an (4.03 × 10^5 cells m^{-3}). Qingdao also had a greater microorganism concentration than Xi′an during the four seasons. In addition, Mu et al. (2020) compared environmental samples from urban and mountainous regions in Xi′an,

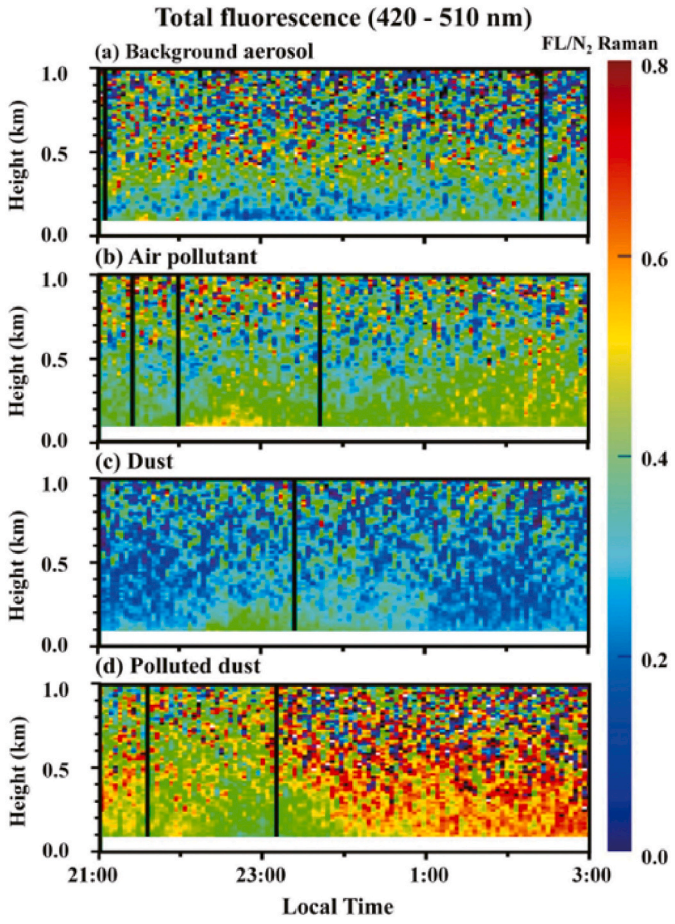

Fig. 5. Vertical structure of total fluorescence signals between 420 and 510 nm for four typical aerosols: background aerosols (a), air pollutant (b), dust (c) and polluted dust (d) during April 2014 in Linze (100.12°E, 39.05°N), China. From Wang et al. (2023).

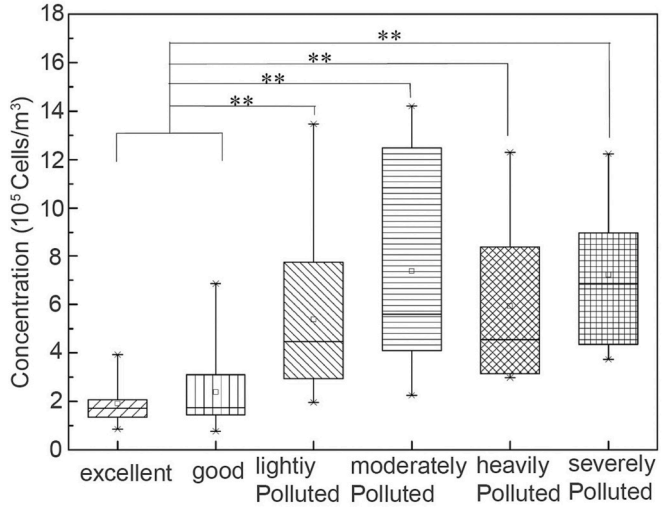

Fig. 6. Example of total airborne microbe concentrations at different air quality levels. The box frames represent the upper quartile and lower quartile, the line represents the median, the whiskers denote the range, and "o" represents the mean. "**" indicates a statistically significant difference between concentrations. From Xie et al. (2018b).

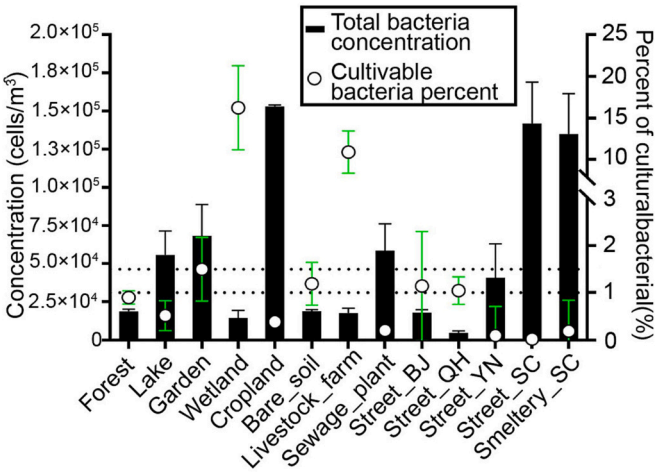

Fig. 7. Example of the concentration of total airborne bacteria and culturable bacteria for various land use types. From Li et al. (2020).

indicating that microbial concentrations were somewhat greater in the latter.

4. Influencing factors

4.1. Emission sources

Bioaerosols are mostly emitted from natural and human activities (Fig. 8). Biological particles usually enter the atmosphere via exposed surfaces, such as soil, deserts, natural water bodies (rivers, oceans, etc.), vegetation leaf surfaces, plant and animal metabolites (Bertolini et al., 2013; Bowers et al., 2011a; Bowers et al., 2011b; Jones and Harrison, 2004; Li et al., 2016; Smets et al., 2016; Xie et al., 2021; Xu et al., 2017). Bioaerosols remain in the atmosphere before they are removed by wet and dry depositions (Burrows et al., 2009b). Therefore, local airborne bioaerosol concentration is directly related to emission sources and emission amount during the sampling period. Differences in emission sources and emission amount under different underlying surfaces, seasonal, weather and other conditions are important reasons for variations in bioaerosol concentrations. Soil is the main natural source of terrestrial bioaerosols (Barberán et al., 2015; Gandolfi et al., 2015; Li et al., 2019; Xie et al., 2021; Xie et al., 2018b) because it provides favorable growth medium and nutrients. The contribution of the soil source may be more prominent during the cold season (Bowers et al., 2011a; Xu et al., 2017) and hazy events (Huang et al., 2014; Xie et al., 2018b). Wave breaking and bubble bursting in seawater generate microorganisms, increasing the sea source composition of air in nearby terrestrial and aquatic environments. Marine biological sources may be dominant in the near-surface air of distant marine regions (Li et al., 2011; Liu et al., 2008; Tomasi et al., 2017; Xu et al., 2011). In general, the amount of pollen and fungal spores in the plant growing season and vegetation cover areas are generally high (Lymperopoulou et al., 2016). Emissions from plants and animals are significant because they spread germs that can cause illness in humans, such as allergies and infections. Human activities also contribute significantly to bioaerosol generation. Indoor facilities such as air conditioners and vacuum cleaners, hospital activities, building surfaces (damp and mold) and the human body contribute most of the indoor bioaerosols (Delanoë et al., 2020; Gołofit-Szymczak et al., 2019; Karimpour Roshan et al., 2019; Rai et al., 2021; Stockwell et al., 2019). Areas of intensive human activities (e.g., agricultural fields, farms, sewage treatment plants, smelters and landfills) have been found to have higher emission levels than places that are less affected by human activities (e.g., forests and wetlands) (Chow et al., 2015; Frączek et al., 2017; Hurtado et al., 2014; Li et al., 2020; Szyłak-Szydłowski et al., 2016; White et al., 2019).

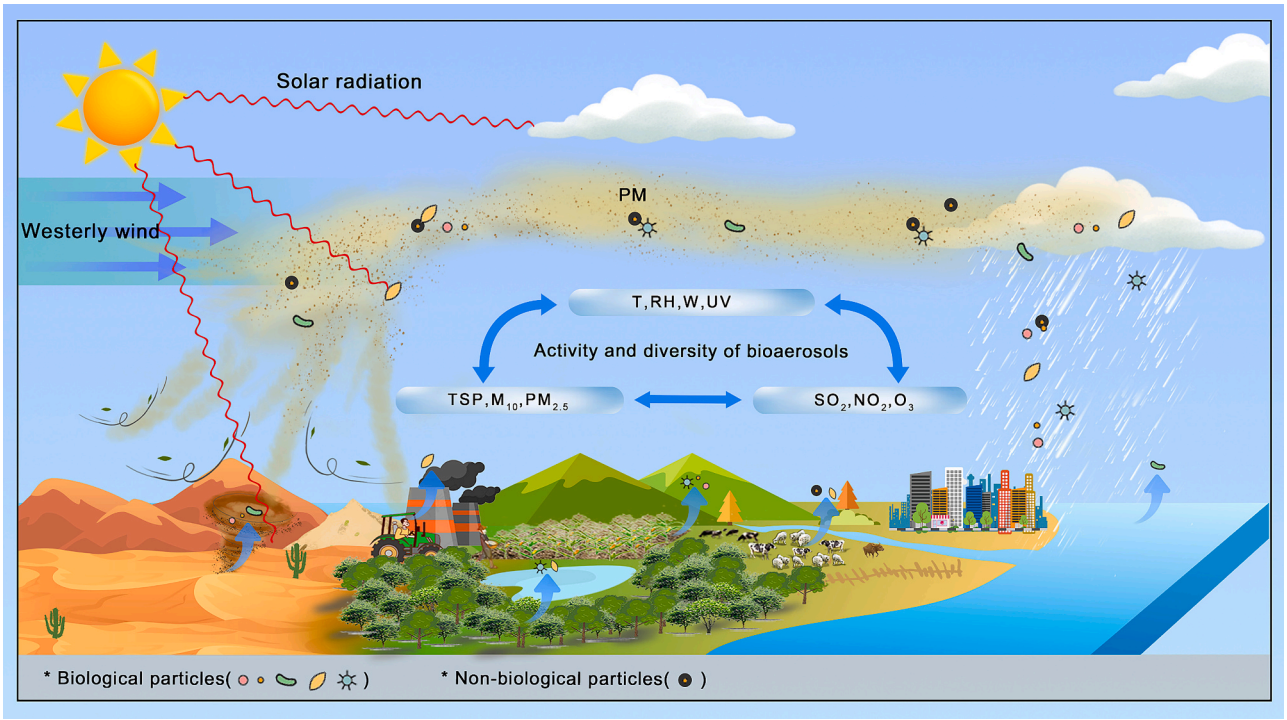

Fig. 8. Schematic diagram of bioaerosols sources and transportation in the atmosphere, as well as their influencing factors.

4.2. Meteorological and environmental factors

A lot of studies have demonstrated that meteorological factors importantly effect on bioaerosols (Estillore et al., 2016; Heo et al., 2014; Jones and Harrison, 2004; Yan et al., 2019; Zhong et al., 2016), as presented in Fig. 8 and Table 2. These factors affect various types of microbial communities in different ways and degrees. Temperature affects atmospheric bioaerosols directly or indirectly. On the one hand, temperature directly affects the viability of microorganisms. Low temperature reduces the fluidity of cell membranes and the activity of microbial enzymes, thereby inhibiting microbial growth and reproduction; high temperature affects the state and integrity of proteins and genomes, such as temperatures above 24 °C may reduce the survival rate of airborne bacteria (Slonczewski et al., 2009; Tang, 2009; Xie et al., 2018b; Zhong et al., 2016). The suitable temperature ranges are different for the survival of psychrophiles, mesophiles, and thermophile. Most microorganisms have high concentrations at moderate values of temperature (Grinn-Gofroń et al., 2018). The temperature is usually positively correlated with microbial concentration in the suitable range (Hwang and Park, 2014; Li et al., 2011; Salonen et al., 2015). Huang et al. (2020) found that the concentration of SARS-CoV-2 increased significantly in the optimal temperature zone. In addition, temperature also indirectly affects atmospheric bioaerosols in other ways. For example, when an inversion layer occurs, a stable stratification is formed. This phenomenon weakens the diffusion of bioaerosols in the atmosphere.

Air humidity usually affects the bioaerosols themselves directly or indirectly affects bioaerosols in aerodynamic behavior. Different microorganisms might benefit from or be inhibited by the same levels of relative humidity. In terms of bioaerosols sources, the inert and active release processes of fungal spores are closely related to humidity. The humidity and temperature of the air, as well as the radiation balance of the surface, will determine the bonding effects of the particles and ultimately influence the inert release of the bioaerosols (Jones and Harrison, 2004). The inert release of many fungal conidia is associated with a decrease in relative humidity, e.g., *Bremia lactucae*, *Alternaria alternata*, etc. (Su et al., 2000; Timmer et al., 1998). Most ascospores and

Table 2
Influence mechanism of meteorological and environmental factors on bioaerosols.

Impact factor	Action mechanism	Ref
Temperature	Inversion layer prevents diffusion	(Zhong et al., 2016)
	Low temperature reduces microbial activity	(Slonczewski et al., 2009)
	High temperature affects the integrity of proteins and genomes	(Tang, 2009)
Humidity	Preventing diffusion	(Burch and Levetin, 2002)
	Inert release processes	
	Active release of spores	(Jones and Harrison, 2004)
	Promoting dry deposition	
	Influencing microbial activity	(Xie et al., 2018b) (Zhai et al., 2018)
Wind	Dilution	(Cowherd, 1990)
	Change transmission path	(Jones and Harrison, 2004)
	Inert release and mechanical movement	(Smith et al., 2012)
Particulate matter	Attached carrier	(Adhikari et al., 2006)
	Toxic/promotional effects	
	Change the morphological, biological and aerodynamic characteristics of bioaerosols	(Innocente et al., 2017) (Abdel Hameed et al., 2012)
Solar radiation	Key environmental factor for DNA damage	(Pan et al., 2021)
Precipitation	Active release	(Christner et al., 2008)
	Attached carrier	
	Scouring and washing	(Jones and Harrison, 2004)
	Favorable survival environment	
	Inert release processes and resuspension	(Heo et al., 2014)
O_3	Phototoxic oxidant, antibacterial activity	(Tiedemann and Firsching, 2000)
SO_2, NO_2	Nutrients	(Deng et al., 2010)
	Destroy biological structure	(Ehrlich and Miller, 1972)
	Participate in the synthesis toxic pollutants	(Harrison and Perry, 1986)

basidiospores are actively released after the surface has been wetted (Jones and Harrison, 2004). High relative humidity and precipitation promote the process. Basidiospore concentrations are more directly affected by relative humidity (Burch and Levetin, 2002). Zhai et al. (2018) noted that humidity values of 70 %–80 % were particularly favorable for the release of ascospores and basidiospores. In contrast, spore types such as *Cladosporium*, *Alternaria*, *Epicoccum*, and *Dreschlera* tend to have higher concentrations in warm and dry weather (Burch and Levetin, 2002). Hygroscopic action and expansion at high relative humidity can also lead to pollen rupture, which promotes the production of biofragments (Huffman et al., 2013; Rathnayake et al., 2017). Relative humidity also directly affects microbial activity. Most Gram-positive bacteria easily survive under high relative humidity, while Gram-negative bacteria prefer low relative humidity (Xie et al., 2018a). Higher humidity may be more likely to be detrimental to bacteria in dust (e.g., *Staphyloeoccus aureus* and *Streptococcus pyogenes*), whose mortality rates were positively correlated with atmospheric humidity (Lidwell and Lowbury, 1950). Aerosolized influenza viruses also survived shorter at higher humidity (50–90 %) (Hemmes et al., 1960). From the perspective of aerodynamic behavior, high relative humidity during sunny days prevents dust lifting, thus reducing the amount of bioaerosols entering the atmosphere. High relative humidity also prevents the diffusion behavior of bioaerosols. At the same time, high relative humidity in conjunction with the property of suspended particles to absorb moisture promotes dry deposition.

UV irradiation is a key environmental factor for DNA damage (Pan et al., 2021). The maximum microbial inactivation efficiency is usually observed at 254 nm (UVC) (Wang et al., 2019). Intense solar radiation often means stronger UVC radiation, which can inactivate cells. This effect is more obvious for airborne bacteria (Hwang et al., 2010; Kowalski and Pastuszka, 2018).

The role of wind is mainly a function of movement. The diffusion routes of bioaerosols are influenced by wind direction. Downwind brings particles from upwind source areas, causing changes in bioaerosols concentration and composition (Hoose et al., 2010; Lymperopoulou et al., 2016; Murata and Zhang, 2016; Seifried et al., 2015). Prevailing winds are important drivers in the long-range transport of microorganisms (Smith et al., 2012). The westerly belt is a typical example of a natural transport channel. Postfrontal air parcels that follow fast-moving cold fronts in the westerly wind flow are the most efficient microbial conveyor (Murata and Zhang, 2014). Such air parcels frequently move from Asia to North America quasi-conservatively in spring and fall, to the polar region in summer, and to the subtropics areas in winter (Murata and Zhang, 2014). Wind is also a facilitating factor for the release of bioaerosols from various surfaces. The magnitude of wind speed determines the removal effect. The wind speed must be greater than a certain value to have the effect of blowing down or moving particles. In general, the typical threshold wind speed for microbial removal from the ground (3.0–5.4 m/s) was greater than that from plants (0.5–2.0 m/s) (Cowherd, 1990; Xie et al., 2018a). The promotion of microbial release by wind acts mainly on mechanical release after biological damage and inert release. On the other hand, strong winds will dilute local bioaerosols, especially during pollution events (Lighthart and Kim, 1989; Zhen et al., 2017; Zhong et al., 2016).

The effects of precipitation on bioaerosols are characterized by both facilitation and inhibition. First, rainfall promotes inert emission and resuspension of microorganisms. The momentum of fungal spores floating during rainfall comes from the impact of large raindrops or air excluded from the impact zone (Jones and Harrison, 2004). Similar to relative humidity, precipitation also promotes the active release of spores. However, this promotion will expire when the spores are depleted (Jones and Harrison, 2004). Precipitation is required for the release of many ascospores (Burch and Levetin, 2002). When precipitation occurs, bioaerosols at higher altitudes (e.g., in clouds) fall with raindrops (Christner et al., 2008; Kang et al., 2015). At the same time, ultraviolet light decreases and humidity increases, which creates a suitable environment for the growth of most microorganisms. On the other hand, precipitation has scouring and washing effects on airborne particles. Snow covers release sources during the cold season (Schumacher et al., 2013). These effects cause to decline in bioaerosols concentrations. The relative intensity of precipitation in different climates seems to be the dominant issue in determining the removal effect and increasing impact of precipitation on airborne bioaerosols (Heo et al., 2014; Li et al., 2017).

Bioaerosols are also closely related to levels of atmospheric particulate matter and special gases. Airborne microorganisms can attach to suspended particulate matter. Bioaerosols, such as pollen and fungal spores, change their morphological characteristics (Alghamdi et al., 2014; Glikson et al., 1995), biological properties (e.g., allergenicity) (Monn, 2001; Ormstad et al., 1998; Parnia et al., 2002), and aerodynamic characteristics (Abdel Hameed et al., 2012; Adhikari et al., 2006) when bound to particulate matter. And their diffusion is affected. In addition, trace metals, secondary inorganic substances, organic compounds, and other components of particulate matter have toxic or promotional effects on biological particles (Adhikari et al., 2006; Innocente et al., 2017). The bacterial contents of coarse and fine particles are different (Liu et al., 2018; Xu et al., 2017). Thus, the relationship between PM and bioaerosol concentrations is complex (Alghamdi et al., 2014; Haas et al., 2013; Jeon et al., 2011; Raisi et al., 2010; Xie et al., 2018a). Ozone is considered a phototoxic oxidant (Tiedemann and Firsching, 2000) with antimicrobial activity. High concentrations of ozone can kill microorganisms, hence the number of microorganisms is usually negatively correlated with ozone concentrations (Sharma and Hudson, 2008; Wei et al., 2016; Xie et al., 2018b). On the one hand, gaseous air pollutants such as SO_2 and NO_2 can be utilized as nutrients for microorganisms through dissolution in water and chemical conversion to form secondary inorganic substances (Deng et al., 2010; Dong et al., 2016). On the other hand, SO_2 and NO_2 exert a strong toxic effect on microorganisms (Abdel Hameed et al., 2012). SO_2 and NO_2 form nitric acid, sulfuric acid and nitrite, which destroy biological structures (Ehrlich and Miller, 1972). They also react chemically to form more toxic oxidants, compounds and other pollutants that inhibit microbial growth and reproduction (Harrison and Perry, 1986; Won and Ross, 1969).

4.3. Impact mechanisms of special events

Previous studies have shown that dust can be transported thousands of miles across continents (Huang et al., 2015; Liu et al., 2022). Thus, dust is an excellent vehicle for the long-range transport of bioaerosols (Fig. 8). Dust carries exogenous microorganisms to affect the quantity and composition of the downwind region, which leads to bacterial enrichment in the topsoil (Hara and Zhang, 2012; Kellogg and Griffin, 2006; Li et al., 2011; Yamaguchi et al., 2012; Yuan et al., 2017). And the viability of microorganisms can be affected by dust, so most of the bacteria brought in by the dust are not viable (Hara and Zhang, 2012; Yuan et al., 2017). Previous studies have shown that many viable microorganisms were present in dust-generating areas because they form survival mechanisms suitable for the local environment (Hagiwara et al., 2020; Maier et al., 2004; Makhalanyane et al., 2015). These viable bacteria follow dust long-distance transport while also being damaged by the harsh environment (prolonged solar radiation, lack of nutrient depletion, dryness, low temperatures, toxic substances, etc.) and protected by the dust (attachment, shading, provision of nutrients). For many bacteria transported over long distances, destruction is stronger than protection, which leads to their death. However, some bacteria in aerosols are highly pigmented, which protects them from UV radiation; some microorganisms form dormant spores during transport and can tolerate harsh conditions; and certain microbes are highly tolerant of extreme environmental conditions (Kellogg and Griffin, 2006; Nicholson, 2002; Tong and Lighthart, 1997). Therefore, dust also brings a fraction of viable microorganisms in the dust source areas, which is

particularly important in considering pathogen and allergen transmission. Dust devil is a major means of transporting dust aerosols into the atmosphere in summer (Du et al., 2023). The amount of bioaerosols brought into the atmosphere by such dust devils is also of concern.

When fog is present, the relative humidity rises. The right amount of moisture in the air encourages the growth of microorganisms. Larger droplets in the air make it easier for microbes to stick to surfaces and reduce the effects of UV radiation, dehydration, and drying on airborne organisms (Amato et al., 2007a; Amato et al., 2007b; Dimmick et al., 1979; Dong et al., 2016). Moreover, under foggy conditions, the ground temperature decreases, which results a stable atmosphere that enables microorganisms to accumulate easily.

Inhalable particulate matter is the carrier for the growth of atmospheric microbes. When haze occurs, its concentration increases significantly, which also provides more nutrients (e.g., sulfates and nitrates). Under such conditions, solar radiation is weakened, wind speed is low, and the atmosphere is stable; these conditions are favorable for microbial growth and accumulation. Some strains that have adapted to environmental changes become dominant strains on hazy days (Dong et al., 2016; Li et al., 2018). Moreover, high concentrations of toxic and harmful substances (heavy metal elements, polycyclic aromatic hydrocarbons, inorganic ions, etc.) on hazy days cause damage to microorganisms (Gao et al., 2015; Xie et al., 2018a). The competition between pro-growth (accumulation) effects and toxic effects determines the trend of increasing or decreasing microbial concentrations. From the air quality index perspective, some studies (Liu et al., 2018; Xie et al., 2018b) pointed out that the pro-growth effect was stronger before moderate pollution and turned weaker afterward.

When special weather occurs, the atmospheric environment is necessarily altered. Fundamentally, the changes in bioaerosols remain due to a combined effect of sources and meteorological factors.

5. Conclusion and future perspectives

Previous studies have shown that bioaerosols play a significant role in atmosphere-biology-hydrology interactions. Despite the development of various bioaerosol-related technologies, detection remains a great challenge. The advantages, disadvantages and scope of application of detection methods have been discussed. Choosing the right method will undoubtedly help to increase the accuracy of detecting bioaerosols. However, the current selection of these methods is subjective. Sampling and detection methods currently used by different researchers in the field of atmospheric bioaerosols are different, enhancing the difficulty of comparing data. Therefore, standard sampling procedures and detection systems should be established to provide a uniform research basis. The existing offline detection methods for bioaerosols are more accurate. However, the results are often slow and labor-intensive. In contrast, online methods are relatively fast and convenient. A combination of multiple technologies is expected to reduce interference to a greater extent and to enhance the efficiency of detecting bioaerosols in complex atmospheric backgrounds. With the emergence of the COVID-19 pandemic, the real-time monitoring of airborne microbes has become an urgent issue. However, the concentration of airborne viruses is usually low, and conventional collection methods have resulted in some degree of microbial inactivation. It is necessary to develop new tools (e.g., biosensors) with the advantages of fast response, low cost and easy integration.

The sources of bioaerosols vary greatly under different conditions. Furthermore, meteorological and environmental factors affect atmospheric bioaerosols through multiple processes and complex synergistic effects. As a result, the concentration of bioaerosols in the atmosphere exhibits obvious spatial and temporal patterns. We sorted these distribution characteristics and influence mechanisms. To obtain accurate warning information on bioaerosols, more observational data are needed. At present, bioaerosol sampling is mostly limited to small scale regions. There is a lack of continuous observation data across space and time. Long-term monitoring, expansion of the sampling range and establishment of a monitoring network platform are conducive to an in-depth investigation of the overall spatial and temporal variation in global bioaerosol concentrations. In addition, more chamber experiments and field observations should be conducted to establish bioaerosol emission inventories at a large scale. These progresses may provide the cornerstone for investigating emission fluxes, transportation, and impacts of bioaerosols, as well as the basis for a comprehensive understanding of the mechanisms of atmospheric contribution to bioaerosols.

CRediT authorship contribution statement

Zhongwei Huang: Conceptualization, Funding acquisition, Project administration, Writing – review & editing. **Xinrong Yu:** Formal analysis, Visualization, Writing – original draft. **Qiantao Liu:** Visualization, Writing – review & editing. **Teruya Maki:** Writing – review & editing. **Khan Alam:** Writing – review & editing. **Yongkai Wang:** Visualization. **Fanli Xue:** Writing – review & editing. **Shihan Tang:** Writing – review & editing. **Pengyue Du:** Formal analysis. **Qing Dong:** Formal analysis. **Danfeng Wang:** Writing – review & editing. **Jianping Huang:** Conceptualization, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Can request from the author

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