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ABSTRACT

Atmospheric aerosol particles of biological origin are a very diverse group of biological materials and structures, including microorganisms, dispersal units, fragments and excretions of biological organisms. In recent years, the impact of biological aerosol particles on atmospheric processes has been studied with increasing intensity, and a wealth of new information and insights has been gained. This review outlines the current knowledge on major categories of primary biological aerosol particles (PBAP): bacteria and archaea, fungal spores and fragments, pollen, viruses, algae and cyanobacteria, biological crusts and lichens and others like plant or animal fragments and detritus. We give an overview of sampling methods and physical, chemical and biological techniques for PBAP analysis (cultivation, microscopy, DNA/RNA analysis, chemical tracers, optical and mass spectrometry, etc.). Moreover, we address and summarise the current understanding and open questions concerning the influence of PBAP on the atmosphere and climate, i.e. their optical properties and their ability to act as ice nuclei (IN) or cloud condensation nuclei (CCN). We suggest that the following research activities should be pursued in future studies of atmospheric biological aerosol particles: (1) develop efficient and reliable analytical techniques for the identification and quantification of PBAP; (2) apply advanced and standardised techniques to determine the abundance and diversity of PBAP and their seasonal variation at regional and global scales (atmospheric biogeography); (3) determine the emission rates, optical properties, IN and CCN activity of PBAP in field measurements and laboratory experiments; (4) use field and laboratory data to constrain numerical models of atmospheric transport, transformation and climate effects of PBAP.

Keywords: primary biological atmospheric aerosol, climate, cloud condensation nuclei, biology, atmospheric ice nuclei

Contents

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1

1. Introduction

1.1. History

The occurrence and relevance of airborne biological particles have been addressed since the beginnings of scientific investigations into atmospheric aerosols (Ehrenberg, 1847; Pasteur, 1861; Carnelly et al., 1887; De Bary, 1887). For example, by the late nineteenth century, Miquel (1883) had already shown that airborne spore concentrations in France followed a seasonal cycle and were dependent on wind direction. He also showed that human mortality in Paris followed the bacteria concentration in the air. Since then, aerobiology (i.e. the study of airborne biological particles) has become well established as a multidisciplinary field of scientific research that interacts with a host of physical, biological and medical science disciplines (e.g. Gregory, 1973). The impact of aerobiology is especially notable in such diverse basic and applied sciences such as allergology, bioclimatology, palynology, biological pollution, biological warfare and terrorism, mycology, biodiversity studies, ecology, plant pathology, microbiology, indoor air quality, biological weathering, industrial aerobiology and cultural heritage.

The potential relevance of biological particles for atmospheric processes has also been recognised for many years (e.g. Dingle, 1966; Schnell and Vali, 1972; Jaenicke and Matthias, 1988; Matthias-Maser and Jaenicke, 1995; Andreae and Crutzen, 1997; Jaenicke, 2005; Pöschl, 2005). Figure 1 outlines major processes in the cycling of primary biological aerosol particles (PBAP)[1] between atmosphere and biosphere. After emission from the biosphere, PBAP undergo various physical and chemical aging processes in the atmosphere (coagulation, surface coating, reaction with photo-oxidants, etc.). Depending on their surface properties, PBAP can serve as nuclei for water droplets or ice crystals, leading to the formation of clouds and precipitation. Removal from the atmosphere proceeds via dry deposition (diffusion/sedimentation) or wet deposition with precipitation (nucleation/scavenging). After deposition, PBAP can interact with terrestrial or aquatic ecosystems and trigger biological activities leading to further PBAP emissions (growth and reproduction). However, biological particles in general have received less

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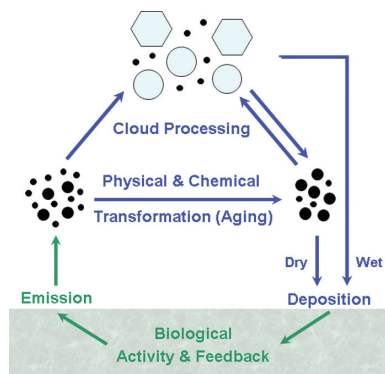[1]A list of abbreviations can be found in the appendix.

Fig. 1. Cycling and effects of primary biological aerosol particles in the atmosphere and biosphere (adapted from Pöschl, 2005).

attention in atmospheric science than other types of aerosol particles such as sulfate, sea salt, mineral dust or volcanic ash (e.g. Junge, 1963; Hammond, 1971; Friedlander, 2000). This is primarily because the atmospheric impact of biological aerosols has been poorly understood, and because atmospherically relevant measurements have been costly and difficult to interpret. Also, global average number concentrations of biological particles have often been assumed to be insignificant compared to non-biological material and have thus not typically been considered for widespread measurements or included in global climate models. The Third Assessment Report (TAR) of the Intergovernmental Panel on Climate Change (IPCC) in 2001, for example, listed the global source strength of primary biological aerosol particles to be only 56 Tg/yr, in contrast to 3340 Tg/yr for sea salt and 2150 Tg/yr for mineral dust listed in the same report (Penner et al., 2001). Furthermore, the Fourth Assessment Report of the IPCC in 2007 stated that these estimates had not been refined, and primary biological particles were not mentioned in the contribution of Working Group I (Physical Science Basis) to the overall report (IPCC 2007b). PBAP concentrations have been estimated by other researchers (e.g. Matthias-Maser and Jaenicke, 1995) as comprising a much higher percentage of total atmospheric aerosol volume, however, and so important discrepancies exist.

Interest in biological aerosol has been growing significantly in recent decades. This is highlighted by the fact that an Institute for Scientific Information (ISI) search for the term 'biological aerosol' (including quotation marks) results in less than a total of five publications until 1987, approximately one citation per year between 1987 and 1998, and then steadily increasing numbers with an average of ~ 9 citations per year between 1998 and 2011. Recently, several investigations have suggested that biological particles can have a substantial influence on clouds and precipitation and thus may influence the hydrological cycle and climate at least on regional scales (e.g. Andreae and Rosenfeld, 2008; Prenni

et al., 2009; Pöschl et al., 2010). Various fields of medical research are also concerned with biological aerosols. Biological particles have been linked to many different adverse health effects spanning from infectious diseases to acute toxic effects, allergies, asthma and even cancer (Peccia et al., 2011). The negative effects that bioaerosols can play on the human respiratory system are particularly well documented (Verhoeff and Burge, 1997; Burge and Rogers, 2000; Douwes et al., 2003; Lee et al., 2005). Although medical research dealing with biological aerosols is indeed critical, this review article does not discuss medical applications of biological aerosols directly, providing instead a synthesis and overview of recent studies dealing with the observation and relevance of primary biological aerosol particles in an atmospheric context.

1.2. Definition and sources of primary biological aerosol particles

Aerosols are generally defined as colloidal systems of liquid or solid particles suspended in a gas (Hinds, 1999; Baron and Willeke, 2001; Fuzzi et al., 2006). Particle diameters are typically in the range of ~ 1 nm to around ~ 100 μm, where the lower limit is given by the size of small molecular clusters and the upper limit by high settling velocities comparable to the magnitude of atmospheric updraft velocities ($\sim 1\,\mathrm{m\,s}^{-1}$, Hinds, 1999; Seinfeld and Pandis, 2006). Primary atmospheric aerosol particles are emitted directly into the atmosphere from a source material, whereas secondary particles are formed in the atmosphere by condensation of gaseous precursors (Pöschl, 2005; Fuzzi et al., 2006).

The term 'primary biological aerosol particles' is defined to describe solid airborne particles derived from biological organisms, including microorganisms and fragments of biological materials such as plant debris and animal dander (IGAP, 1992)[2]. The definition for PBAP used within the text, as outlined in Table 1, can thus include all sorts of intact or fragmented biological cells, dispersal units or tissues.

The term primary biological aerosol is more or less equivalent to the 'soft' term 'bioaerosol' (Reponen et al., 1995; Hinds, 1999). In contrast to the more rigorously defined 'biological aerosol', however, the term 'bioaerosol' is not very clearly defined and is frequently used with different meanings. In some cases, the term bioaerosol is used in a rather narrow sense, excluding biological secretion such as plant wax particles, for example (Gelencér, 2004). In other cases, it is used in a very broad sense, e.g. including any particle with biological activity/toxicity

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[2]Originally defined by Griffith, W. D.; Jaenicke, R.; Levin, Z.; Matthias-Maser, S; Rantio-Lehtimaki, A.; Schnell, R. C.; and Sinha, M. P.

Table 1. Characteristic types of primary biological aerosol particles (PBAP)

Particle types	Examples
Biological organisms or dispersal units (dead or alive, isolated or aggregated)	Bacteria, fungi, protozoa, algae, spores, pollen, lichen, archaea, viruses, etc.
Solid fragments or excretions of biological organisms or dispersal units	Detritus, microbial fragments, plant debris/leaf litter, animal tissue and excrements, brochosomes, etc.

(Hirst, 1995), which would theoretically also comprise droplets of toxic chemicals such as sulphuric or nitric acid. Moreover, the term primary biological aerosol enables clear and easy distinction from biogenic secondary organic aerosols that are formed by atmospheric oxidation and gas-to-particle conversion of volatile organic compounds released from biological organisms (Hallquist et al., 2009; Jimenez et al., 2009). Therefore, we use the term biological aerosol within this review for the types of particles outlined in Table 1.

The size of PBAP can range from several nanometers (e.g. viruses, cell fragments) to a few hundred micrometres in aerodynamic diameter (e.g. pollen, plant debris; Cox and Wathes, 1995; Hinds, 1999; Jaenicke, 2005; Pöschl, 2005). Larger particles of biological material can also be lifted into the air, but due to high settling velocities they are rapidly deposited rather than being suspended over long times. Thus, they are usually not considered to be atmospheric aerosol particles, which is also the case for self-propelled organisms.

The biosphere, or the system in which all living things interact, dominates the Earth's surface, influencing the composition of land, water and air. Thus, PBAP can be released, both actively and passively, from every region of the globe. Key PBAP-producing systems include the following.

Plants release PBAP in the course of decay processes (see Section 2.7) as well as for reproduction, including pollen from higher plants and spores from ferns and mosses (see Section 2.3).

Microorganisms inhabit most plant, soil and rock surfaces (see Sections 2.1, 2.2, 2.5, 2.6). These microorganisms can be very numerous, contributing huge number concentrations per unit surface area ($10^4 - 10^8$ cells cm^{-2}) in various natural environments (Morris and Kinkel, 2002; Lindow and Brandl, 2003; Yadav et al., 2004). Furthermore, the global leaf surface area is estimated to be roughly four times the terrestrial ground surface area ($\sim 6.4 \ 10^8$ km^2 vs. $\sim 1.5 \ 10^8$ km^2) that provides a correspondingly large surface area for PBAP emission (Whittaker and Likens, 1973).

Primary biological aerosol particles originating from animals and humans include debris from skin or hair as well as, for example, excrements, brochosomes and eggs dispersed into the atmosphere by insects (see Section 2.7).

In areas of human activity, such as cities or agricultural managed areas, the numbers and composition of microorganisms such as bacteria or fungi are often increased and altered with respect to rural areas (see Sections 2.1.1, 2.2).

The cryosphere (e.g. Greenland, Antarctica, glaciers) is formed largely from precipitation, and this may be triggered by PBAP in some situations (Sands et al., 1982; Christner et al., 2008b; Pöschl et al., 2010). Bacteria have been discovered in ice cores from Antarctica at depths up to 3519 m (Raymond et al., 2008), giving possible evidence to the idea that these organisms have been introduced through precipitation. Thus, surface snow under wind-blown conditions could be a powerful source for PBAP via resuspension (Pomeroy and Jones, 1996).

Roughly, 70% of the globe is covered by oceans. They are full of living and decaying organisms, such as bacteria, archaea, fungi and algae, that are ejected from the ocean surface by bubble-bursting mechanisms, similar to the way other particles (e.g. sea salt) are emitted from such surfaces (Blanchard, 1983; O'Dowd et al., 2004).

In summary, the earth's biosphere provides many diverse and important sources of PBAP. We begin this review by discussing seven major categories of atmospherically relevant biological particles in detail. This is followed by a survey of available methods for PBAP detection and analysis, and overviews of the general atmospheric relevance of PBAP and their optical properties.

2. Characteristic types of primary biological aerosol particles

2.1. Bacteria and archaea

Due to their small size, bacteria have a relatively long atmospheric residence time (on the order of several days or more) compared to larger particles and can be transported over long distances (up to thousands of kilometres). Measurements show that mean concentrations in ambient air can be greater than 1×10^4 cells m^{-3} over land (Bauer et al., 2002a), whereas concentrations over the sea may be lower by a factor of $\sim 100 - 1000$ (Prospero et al., 2005; Griffin et al., 2006). Airborne bacteria may be suspended as individual cells but are more likely to be attached to other particles, such as soil or leaf fragments, or found as agglomerates of many bacterial cells (Bovallius et al., 1978; Lighthart, 1997). For this reason, whereas individual bacteria are typically on the order of ~ 1 μm or less in size, the median aerodynamic diameter of particles containing

culturable bacteria at several continental sites has been reported to be ∼4 µm, whereas at coastal sites it is ∼2 µm (Shaffer and Lighthart, 1997; Tong and Lighthart, 1999; Wang et al., 2007).

The analysis of the diversity, composition and abundance of bacteria in air has experienced a recent growth in interest within the aerosol community (Morris et al., 2011). Understanding of the presence or properties of airborne bacteria is important because bacteria can influence atmospheric processes, function as human, plant and animal pathogens and be distributed over large physical scales from their natural or anthropogenic sources. In addition, the prediction of behavioural changes in bacterial colonisation of remote environments may be linked to climatic or anthropogenic changes that influence the atmosphere and thus could be a useful marker of changes in biodiversity.

Although in recent years, research on bacteria in the atmosphere has been constantly expanding, it remains difficult to establish a clear picture of the actual abundance and composition of bacteria in the air (Mancinelli and Shulls, 1978; Grinshpun and Clark, 2005; Maki et al., 2010). The presence of bacteria in air is strongly dependent on many factors such as seasonality, meteorological factors, anthropogenic influence, variability of bacterial sources and many other complicated variables. More importantly, the analysis of airborne bacteria still suffers from a lack of standardisation in air sampling and sample processing methods (Kuske, 2006; Peccia and Hernandez, 2006; Womack et al., 2010). Thus, differences in airborne concentration estimates, as well as in composition and abundance, could either be caused by biological variations or by differences in sampling or analysis strategies. Furthermore, many airborne bacteria studies were not designed to study a broad range of species but only to detect specific, and often pathogenic, species. Thus, current understanding of airborne bacteria concentrations and properties is undoubtedly influenced by such studies, and the literature should be understood with this in mind.

One area of expanding research is work towards the use of specific bacterial species for 'source tracking', conceptually similar to other atmospheric tracer methods. For example, the relative contribution of bacteria from various source environments can be determined, thus allowing measurements at an individual measurement site to predict the history of the air arriving at that location. Bowers et al. (2010) made a contribution in this direction by identifying groups of bacteria in atmospheric samples, which are typically found primarily in the soil or on leaf-surface environments.

2.1.1. Urban airborne bacteria. The analysis and comparison of bacteria between urban and other environments has focused mostly on the comparison of bacterial concentration and not on diversity estimates. Historically, bacteria have typically been divided into Gram-positive and Gram-negative bacteria depending on their behaviour when their cell walls are treated by Gram staining. Culturing methods in general find more Gram-positive bacteria (e.g. Mancinelli and Shulls, 1978; Atlas and Bartha, 1997; Atlas and Bartha, 1997; Fuzzi et al., 1997; Kellogg and Griffin, 2006; Amato et al., 2007b; Fang et al., 2007; Fahlgren et al., 2010), whereas culture-independent techniques primarily find Gram-negative bacteria (e.g. Radosevich et al., 2002; Maron et al., 2005; Brodie et al., 2007; Després et al., 2007; Fierer et al., 2008; Fahlgren et al., 2010). Independent of the choice of detection method, several general trends can be observed from ambient measurements. A small number of existing studies suggest that both in urban and in natural areas, airborne bacterial communities are highly diverse, and variations in their species diversity are more complex than had previously been supposed (Bovallius et al., 1978; Jones and Cookson, 1983; Chihara and Someya, 1989). Bacterial diversity in rural areas is generally higher than at urban sites (Després et al., 2007). Still, the concentration of bacteria seems often to be higher in urban than in rural environments (Bovallius et al., 1978; Chihara and Someya, 1989; di Giorgio et al., 1996; Shaffer and Lighthart, 1997; Fang et al., 2007; Fahlgren et al., 2010), even when the samples are taken in the same geographic region. However, opposite trends have also been found: For example, Rosas et al. (1993) described that bacterial concentrations in rural environments are higher than in urban sites. There is also evidence that the bacterial concentrations in the urban environment are influenced by human activities (Bovallius et al., 1978; Fang et al., 2007). Different cities do vary in their bacterial composition and abundance (Brodie et al., 2007); thus, there can be no single, typical description of urban bacterial composition.

A detailed description of the composition of bacteria found in urban air is restricted to only a few studies, as most culture-based studies classify cultured bacteria only as Gram positive or Gram negative, or as cocci or rods but do not provide taxonomic identification. Other studies dealing with the analysis of urban airborne bacteria give only the number of colony forming units (CFU) or other concentration estimates and do not try to identify the bacteria at all. Still, the general trend from available reports is that bacteria found in the air often belong to groups that are also common soil bacteria: on the taxonomic level of phyla, the *Firmicutes* (Table 2),[3] *Proteobacteria, Actinobacteria*

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[3]Table 2 provides an overview of all taxonomic terms used in the review

Table 2. Taxonomic information on biological particles in air mentioned in the review

Kingdom	Superphylum	Phylum	Class	Order	Family	Genus	Species
Bacteria		Firmicutes	Bacilli	Bacillales	Bacillaceae	Bacillus	*Bacillus subtilis*
Bacteria		Proteobacteria	Alphaproteobacteria	Sphingomonadales	Sphingomonadaceae	Sphingomonas	*Sphingomonas echinoides*
Bacteria			Betaproteobacteria				
Bacteria			Gammaproteobacteria	Pseudomonadales	Pseudomonadaceae	Pseudomonas	*Pseudomonas syringae* (which is also the main component of Snomax)
Bacteria							*Pseudomonas fluorescens*
Bacteria							*Pseudomonas viridiflava*
Bacteria							*Pseudomonas antarctica*
Bacteria					Moraxellaceae	Acinetobacter	
Bacteria						Psychrobacter	
Bacteria				Enterobacteriales	Enterobacteriaceae	Pantoea	*Pantoea agglomerans* (formally called *Enterobacter agglomeransor Erwinia herbicola*)
Bacteria						Pectobacterium	*Pectobacterium carotovorum* (formally called *Erwinia carotovora*)
Bacteria						Escherichia	*Escherichia coli*
Bacteria				Xanthomonadales	Xanthomonadaceae	Xanthomonas	
Bacteria						Luteimonas	
Bacteria						Stenotrophomonas	
Bacteria			Deltaproteobacteria				
Bacteria			Epsilonproteobacteria				
Bacteria	Chlamydiae/ Verrucomicrobia group	Verrucomicrobia					
Bacteria	Bacteroidetes/ Chlorophobi group	Bacteroidetes	Bacteroidia				
			Flavobacteria	Flavobacteriales	Flavobacteriaceae	Flavobacterium	
Bacteria		Cyanobacteria		Chroococcales		Chroococcus	*Chroococcus limenticus*
Bacteria		Cyanobacteria		Nostocales	Nostocaceae	Nostoc	*Nostoc Muscorum*
Bacteria		Cyanobacteria		Oscillatoriales		Lyngbya	*Lyngbya lagerheinii*
Bacteria		Cyanobacteria		Oscillatoriales	Phormidiaceae	Phormidium	*Phormidium fragile*
Bacteria		Cyanobacteria		Oscillatoriales		Schizothrix	*Schizothrix purpurascens*

Table 2 (*Continued*)

Kingdom	Superphylum	Phylum	Class	Order	Family	Genus	Species
Bacteria	Fibrobacteres/ Acidobacteria group	Acidobacteria					
Bacteria		Planctomycetes					
Bacteria		Chlorophlexi					
Bacteria		Actinobacteria	Actinobacteria	Actinomycetales	Microbacteriaceae	Microbacterium	
Bacteria					Micrococcaceae	Arthrobacter	*Arthrobacter agilis*
Bacteria					Pseudonocardiaceae	Saccharomonospora	*Saccharomonospora viridis*
Bacteria					Streptomycetaceae	Streptomyces	*Streptomyces albus*
Fungi		Basidiomycota					
Fungi		Ascomycota	Dothideomycetes	Capnodiales	Davidiellaceae	Cladosporium	*Cladosporium cladosporioides*
Fungi							*Cladosporium herbarum*
Fungi			Eurotiomycetes	Eurotiales	Trichocomaceae	Penicillium	*Penicillium brevicompactum*
Fungi							*Penicillium chrysogenum*
Fungi							*Penicillium digitatum*
Fungi							*Penicillium frequentes*
Fungi							*Penicillium melinii*
Fungi							*Penicillium minioluteum*
Fungi							*Penicillium notatum*
Fungi						Aspergillus	*Aspergillus flavus*
Fungi							*Aspergillus fumigates*
Fungi							*Aspergillus versicolor*
Fungi						Paecilomyces	*Paecilomyces variotii*
Fungi			Leotiomycetes	Erysiphales	Erysiphaceae	Blumeria	
Fungi			Sordariomycetes	Hypocreales	Nectriaceae	Fusarium	*Fusarium avanaceum*
Fungi							*Fusarium acuminatum*
Fungi							*Fusarium oxysporum*
Fungi							*Fusarium tricinctum*
Fungi				Microascales	Microascaseae	Microascus	*Microascus brevicaulis* (synonym: *Scopulariopsis brevicaulis*)
Fungi		ZygomycotaSubphylum: Mucoromycotina	Zygomycetes	Mucorales	Mucoraceae	Rhizopus	*Rhizopus stolonifera*
Plantae		Chlorophyta	Chlorophyceae				
Plantae		Pinophyta	Pinopsida	Pinales	Pinaceae	Pinus (pine)	
		Angiospermae		Asparagales	Amaryllidaceae	Narcissus	

Table 2 (*Continued*)

Kingdom	Superphylum	Phylum	Class	Order	Family	Genus	Species
				Asterales	Asteraceae	Ambrosia	*Ambrosia artemisiifolia* (common ragweed)
Plantae				Caryophyllales	Amaranthaceae	Amaranthus	
				Ericales	Theaceae	Camellia	*Camellia sinensis* (Chinese tea)
Plantae				Fagales	Betulaceae	Betula (birch)	*Betula occidentalis* (water birch)
Plantae						Alnus (alder)	
Plantae					Fagaceae	Quercus (oak)	
Plantae				Lamiales	Lamiaceae	Salvia (sage)	
Plantae				Malpighiales	Salicaceae	Populus (poplar)	*Populus nigra 'italica'* (Lombardy poplar)
						Salix (willow)	
Plantae				Poales	Poaceae (true grasses)	Agrostis	*Agrostis gigantea* (red top grass)
Plantae					Poaceae (true grasses), subfamily: Pooideae	Poa	*Poa pratensis* (Kentucky bluegrass)
Plantae	Rhodophyta	Porphyridiophyceae		Porphyridiales	Porphyridiaceae	Porphyridium	*Porphyridium aerugineum*
Protista							Seaweed
Protista / Protozoa	Dinoflagellata	Dinophyceae		Peridiniales	Peridiniaceae	Cachonina	*Cachonina Niei*
Chromalveolata	Heterokontophyta	Chrysophyceae		Chromulinales	Chromulinaceae	Ochromonas	*Ochromonus danica*
Chromalveolata	Heterokontophyta	Xanthophyceae					
Archaea	Crenarchaeota						

are often present, and on the level of superphyla the *Cytophaga-Flavo-Bacteroidetes* group is often being the most commonly observed. Additionally, in some studies bacteria from the phyla of *Verrucomicrobia*, *Cyanobacteria*, *Acidobacteria*, *Planctomycetes* and *Chloroflexi* have been detected. Within the airborne bacteria whose classes belong to *Proteobacteria, Gamma-* and *Betaproteobacteria* have been regularly identified, but *Alpha-*, *Delta-* and *Epsilonproteobacteria* have also been observed. Although *Bacilli* have been found often and in high numbers, drawing conclusions from these observations about their relative abundance is difficult due to high short-term variability and biases from the different detection methods.

Concentrations of bacteria in cities exhibit especially high spatial variation because they are released from strong point sources, in contrast to the more spatially homogeneous release from, for example, an agricultural field. Areas with heavy vehicular traffic or sewage pollution have much higher concentrations of airborne bacteria, with a weaker or non-existent seasonal cycle, as compared to concentrations in more naturally influenced areas such as urban parks, forests or coastal sites (e.g. Miquel, 1883; Shaffer and Lighthart, 1997; Harrison et al., 2005; Fang et al., 2007).

The concentrations and composition of bacteria undergo daily, weekly and seasonal changes. It has often been found that numbers are greatest in summer and autumn (Bovallius et al., 1978; Jones and Cookson, 1983; di Giorgio et al., 1996; Tong and Lighthart, 1999; Fang et al., 2007; Kaarkainen et al., 2008), although exceptions exist; Fahlgren et al. (2010) found that bacteria counts at a coastal site were highest in winter, which they attributed to a strong winter marine sea spray source. Over a period of 1 d, bacteria have usually been observed to exhibit a peak airborne concentration in the morning and evening (Lighthart and Shaffer, 1995; Shaffer and Lighthart, 1997; Fang et al., 2007). It has been suggested by Maron et al. (2006) that bacterial communities in cities show temporal variability, in which the daily and weekly variability is mainly influenced by anthropogenic sources, whereas seasonal variations are triggered by climate and atmospheric changes.

2.1.2. Rural airborne bacteria. Among the Gram-positive bacteria observed in rural air, *Firmicutes* and *Actinobacteria* are the prevalent groups, whereas *Proteobacteria* are the most prevalent Gram-negative bacteria (e.g. Lighthart, 1997; Maron et al., 2005; Després et al., 2007; Fang et al., 2007). Rural and urban sampling sites usually differ with regard to bacterial genetic diversity. Studies based on cultivation often find higher counts of CFUs at urban sites compared to rural sites in the same geographic regions (Bovallius et al., 1978; Jones and Cookson, 1983; Chihara and Someya, 1989; di Giorgio et al., 1996; Fang et al., 2007; Fahlgren et al., 2010). In contrast, some studies based on cultivation or deoxyribonucleic acid (DNA) analysis have detected higher diversity at rural than at urban sites (Rosas et al., 1993; Després et al., 2007). Some studies have shown strong correlations between bacteria concentrations at rural sites and meteorological conditions. For example, Lighthart et al. (2009) found that six meteorological factors could account for 96% of the variance in culturable atmospheric bacteria concentrations measured in rural Oregon. Harrison et al. (2005) measured boundary layer concentrations of total atmospheric bacteria at sites in England and found that they increased exponentially as a function of 24-h mean temperature and, except at the coastal site, decreased logarithmically with increasing wind speed, probably due to atmospheric dilution.

Shaffer and Lighthart (1997) found that mean concentrations of culturable bacteria differed between four distinct land-use types chosen for study: urban, forest, rural and coastal. However, Bowers et al. (2010) obtained an apparently contradictory result, finding concentrations to be $10^5 – 10^6 \, \mathrm{m}^{-3}$ of air in each of three distinct land-use types (agricultural fields, suburban areas and forests). The difference could be related to the specific sites chosen, or could be methodological; whereas Shaffer and Lighthart (1997) used cultivation to enumerate bacteria, Bowers et al. (2010) used fluorescent microscopy to count DNA-containing particles in the size range $0.5 – 10 \, \mu\mathrm{m}$ in diameter.

Despite the lack of difference in total bacteria numbers between the sites, Bowers et al. (2010) found that concentrations of high-temperature ice nuclei, as determined by a droplet freezing assay, were on average two and eight times higher in the samples from agricultural areas than from the other two land-use types, which might indicate an agricultural, perhaps biological, source of ice nuclei, but the nature of the ice nuclei was not determined.

2.1.3. Airborne bacteria at marine and coastal sites. Although it has often been shown that airborne bacteria are dominated by bacterial groups that are prevalent in the soil, airborne bacteria, especially at marine and coastal sites, can also originate from marine sources. Bacteria are transmitted from water to the air by the bubble-bursting mechanism (e.g. Blanchard et al., 1981; Blanchard and Syzdek, 1982). Both, laboratory and field studies, have demonstrated that the concentration of bacteria in bubble bursting or sea spray aerosol greatly exceeds the concentration in the water from which the aerosol is produced (Blanchard and Syzdek, 1978; Blanchard et al., 1981; Blanchard and Syzdek, 1982; Blanchard, 1989; Marks

et al., 2001; Aller et al., 2005). The mean atmospheric residence time of bacteria emitted from the oceans is expected to be shorter than for bacteria emitted from land surface due to their quicker removal by precipitation (Burrows et al., 2009b). In comparison with bacterial concentrations in urban and rural environments, CFU counts seem to be in general lower at coastal sites than at inland sites (Bovallius et al., 1978; Shaffer and Lighthart, 1997). Variation in bacterial concentrations over the course of a day can often be explained by considering onshore breezes that generally bring air with fewer bacteria than inland air (Lighthart, 1997).

Most of the studies dealing with the identification of airborne bacteria at marine and coastal sites have been conducted using culture-dependent techniques. However, it has also been shown in culture-independent analyses that bacteria at coastal and marine sites primarily stem from the phyla of the *Proteobacteria*, *Firmicutes* and *Bacteroidetes*. Within the *Firmicutes*, *Bacillus* seems to be prevalent (Shaffer and Lighthart, 1997), whereas within *Proteobacteria* mainly *Alpha*-, *Beta*- and *Gammaproteobacteria* were detected (Fahlgren et al., 2010; Urbano et al., 2011).

Although in general it has been reported that the concentration of bacteria is highest in summer and autumn, while lowest in winter (Vlodavets and Mats, 1958; Pady and Gregory, 1963; Borodulin et al., 2005), local exceptions can be found to this pattern. In a study analysing the airborne bacterial community at a sampling site near the Baltic Sea with mainly marine influenced air, Fahlgren et al., (2010) detected higher CFU values during the winter compared with the summer. Because marine bacteria are ejected into the air along with sea spray aerosol particles, the source of marine bacteria to the atmosphere increases when winds become more powerful, generating more waves and surf, and thus sea spray. As a result, it is likely that marine bacteria are transferred to the atmosphere far more effectively by stronger winter winds (Nilsson et al., 2001; Nilsson et al., 2007; Fahlgren et al., 2010).

Examination of single particles collected in the air above biologically active ocean areas (Arctic and Southern) shows that bacteria are present, but their numbers are dwarfed by the large number of particles consisting of biogenic organic aggregates and colloids (Leck and Bigg, 2005a, 2005b; Bigg, 2007; Bigg and Leck, 2008).

Methodological issues may have confounded previous measurements of bacteria concentrations in marine air using culture methods. The culturability of bacteria in seawater is estimated to be between 0.001 and 0.1%, compared to 0.25% for freshwater and 0.3% for soil (Colwell, 2000). However, Fahlgren et al. (2010) presented evidence that a majority of live airborne marine bacteria collected on the Swedish coast may be culturable on Zobell agar plates, which are based on Baltic seawater. Also, marine bacteria are smaller than land bacteria, with biovolumes often in the range $0.036 - 0.073 \ \mu m^3$ (Lee and Fuhrman, 1987), corresponding to equivalent spherical diameters of $0.20 - 0.26 \ \mu m$. Consistent with the smaller size of marine bacteria, the count median diameter of particles associated with culturable bacteria has been found to be smaller at coastal sites – about $2 \ \mu m$ – compared to about $4 \ \mu m$ at continental sites (Shaffer and Lighthart, 1997; Tong and Lighthart, 2000; Wang et al., 2007).

2.1.4. High altitude airborne bacteria. The presence of bacteria at high altitudes in the atmosphere had already been detected as early as 1861 (Pasteur, 1861). Metabolically active microbes have been detected in air as high as 20–70 km in elevation (Imshenetsky et al., 1978; Griffin, 2004; Wainwright et al., 2004a; Bowers et al., 2009; Womack et al., 2010). Bacteria have been shown to survive long distance transport and also to be able to live and reproduce in airborne particles (Dimmick et al., 1979). Because bacteria metabolise within cloud droplets, some authors have proposed an impact on the chemistry of cloud droplets and air (Amato et al., 2005, 2007a, 2007c; Deguillaume et al., 2008; Vaitilingom et al., 2010). Vaitilingom et al. (2010) showed that biodegradation is more likely to contribute to cloud chemistry at night than during the day because it must compete with photochemistry during the day. Bacteria collected in cloud water samples have been shown to metabolise and reproduce when those samples are incubated in the laboratory, even at supercooled conditions (Sattler et al., 2001; Amato et al., 2007a; Amato et al., 2007c). Sattler et al. (2001) found that generation times varied between 3.6 and 19.5 d, comparable to those of phytoplankton in the ocean. The mean atmospheric residence time of a bacterial cell can be up to about 1 week (Burrows et al., 2009b), but the cell will spend only a small fraction of this time inside of a cloud droplet. Lelieveld and Heintzenberg (1992) estimated that on average, tropospheric air spends about 5–6% of its time in clouds. It is, thus, unlikely that there is a significant primary production of bacteria within cloud droplets.

In addition to the effect of low temperature at high altitudes, it has been discussed repeatedly that air in general is a hostile environment for microorganisms, as they are exposed to UV light, have only small amounts of water available are subject to changing oxygen partial pressure, etc. (e.g. Womack et al., 2010 and references therein). Bacteria found at high altitudes probably either originate from high altitude habitats such as alpine sites, or they were transported to high altitudes with air currents. Rapid upwards transport of bacteria can be the result of storm activity over land and seas, volcanic activity, impact events

and human activity such as weapons testing, aviation and spacecraft launches (Hall and Bruch, 1965; Bucker and Horneck, 1969; Simkin and Siebert, 1994; Kring, 2000; Griffin et al., 2002; Griffin, 2004). One evolutionary strategy for bacteria to survive in such hostile environments is the use of pigments to protect cells from harmful UV radiation. Thus, some studies on the diversity of bacteria in high altitude concentrate on pigmented bacteria (González-Toril et al., 2009).

The number of aerosol particles and PBAP decreases at high altitudes in general, and several studies could show that the diversity of airborne high-alpine bacteria is also reduced in comparison to urban and rural sites (Després et al., 2007; Bowers et al., 2009). These studies as well as others find primarily bacteria belonging to *Proteo-* and *Actinobacteria* as well as *Bacteroidetes* (González-Toril et al., 2009). Within the *Proteobacteria, Gamma-* and *Betaproteobacteria* are the prevalent classes detected. The presence of *Bacillus* species has also been reported from high altitude sites (Griffin, 2004; Maki et al., 2010). Between the different environmental types, bacteria phyla mainly differ in their relative proportions. Additional differences probably exist also on the species and family level.

2.1.5. Bacteria emission fluxes. Only a few studies have attempted to directly measure the surface-atmosphere flux (net rate of emission and deposition) of bacteria. Flux measurements can be made using micrometeorological methods that rely on measuring the vertical gradient of bacteria concentrations in conjunction with gradients of air

velocity, temperature or other parameters. These methods require fast and very short measurements for statistical significance and can be difficult to design, carry out and interpret. Existing estimates of the flux of culturable bacteria to the atmosphere range from 4.7 CFU m^{-2} s^{-1} for a high desert chaparral in Oregon, USA (Lighthart and Shaffer, 1994) to as much as 543 CFU m^{-2} s^{-1} for undisturbed croplands (Lindemann et al., 1982) and much stronger emissions for surfaces disturbed by human behaviour. For example, during harvesting of crops, emissions may be as high as 10^9 CFU m^{-2} s^{-1} (Lighthart, 1984). A first global model study estimates that average emissions from land of 250 m^{-2} s^{-1} (range: 140–380 m^{-2} s^{-1}) would be required to reproduce observed mean concentrations of bacteria in the air (Burrows et al., 2009b; Fig. 2), note that this estimate refers to total as opposed to culturable bacteria. Major obstacles to successful flux measurements include low number concentrations of airborne bacteria and the lack of automated methods for measuring concentrations because concentration measurements must be made continuously and at high time resolution.

2.1.6. Archaea. All known life on earth can be categorised into one of three broad categories: archaea, bacteria and eukarya. As with bacteria, the DNA of archaea is not contained within a cell nucleus (prokaryotes). Little is known about archaea in the atmosphere. They had long been thought to occur only in very restricted, extreme environments, but by now they have been found in a wide variety of habitats (Schleper et al.,
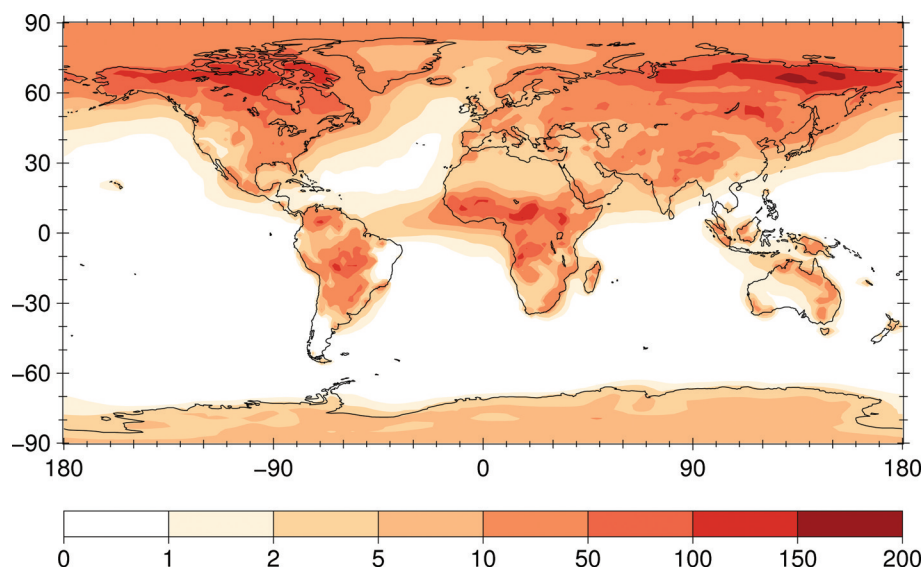

Fig. 2. Column density of bacterial tracer (10^6 m^{-2}), simulated from estimated emissions for a set of ten ecosystems estimates (Burrows et al., 2009b).

2005). They are one of the most diverse and widespread forms of life on Earth and as major players in the biogeochemical cycles of nitrogen and carbon they are involved in the production of methane, the assimilation of amino acids and the oxidation of ammonium (Schleper et al., 2005). Archaea in the atmosphere have thus far been difficult to detect and characterise. Many studies have reported the detection of archaea from samples collected from air above compost piles and biosolids (e.g. Baertsch et al., 2007; Moletta et al., 2007; Thummes et al., 2007), but these are specialised environments rich in biological material. Three aerosol studies (Després et al., 2007; Fierer et al., 2008; Bowers et al., 2009) utilised polymerase chain reaction (PCR) primers capable of amplifying archaeal DNA, but were unable to amplify and detect genetic material from archaea. This may be due to limitations of the applied PCR primers and amplification conditions as described in Section 3.3.1.3. Radosevich et al. (2002) is the only published report to successfully detect DNA sequences of three crenarchaeal clones from ambient air but no further information is provided.

2.2. Fungal spores and fragments

Fungal spores and fragments are understood to be one of the most common classes of airborne PBAP in a number of environments (Womiloju et al., 2003; Elbert et al., 2007; Bauer et al., 2008b; Crawford et al., 2009). Fungi are comprised of vegetative mycelia that consist of a large number of branched hyphae and grow in virtually every ecosystem on Earth and are also capable of efficient aerosolisation (Adhikari et al., 2009). Spores are often released by active processes such as osmotic pressure 'cannons' and surface-tension catapults (e.g. Buller's Drop; Ingold, 1971; Lacey, 1996; Ingold, 1999; Pringle et al., 2005). Spores can be released as a part of the sexual and/or asexual morph (stage) of the lifecycle of a fungus,

and many species are able to produce spores from both stages. Fungi that actively release spores during the sexual morph, or telemorph, can typically produce one of three different kinds of spores: ascospores are released from an ascus (a long tube that typically holds eight spores), basidiospores from a basidium (small pedestal on fruiting bodies) or teliospores. The asexual stage, anamorph, of some fungi produce conidia, also known as conidiospores, that are produced by hyphal portions called conidiophores. Many studies thus refer to spores as a singular class, referring to both sexual and asexual morphs together. Spores are also often subdivided for practical reasons into hyaline (colorless) and dematiaceous (colored) spores (e.g. Pady and Gregory, 1963; Adams et al., 1968). Spores most commonly observed to dominate ambient concentrations of airborne fungal material have been from the species: *Cladosporium*, *Alternaria*, *Penicillium*, *Aspergillus*, as well as *Epicoccum* and a variety of yeasts, smuts and rusts (plant pathogens) and other basidiomycetes (e.g. Madelin, 1994). Detailed reviews on fungal spores in the atmosphere are available elsewhere (e.g. Madelin, 1994; Elbert et al., 2007) and as an example Fig. 3 presents an example of fungal spore micrographs with and without coating by secondary organic aerosol. Some plants such as ferns and mosses also disperse spores that are typically larger and less numerous than fungal spores (Graham et al., 2003; Elbert et al., 2007).

In recent PBAP analyses, molecular genetic methods have been used that analyse the genetic substance, DNA, of biological material. As discussed by Després et al. (2007), fungal DNA detected in aerosol filter samples is most likely to originate from spores that are known to resist environmental stress and survive atmospheric transport (Madelin, 1994; Griffin, 2004; Griffin and Kellogg, 2004). But, fungal DNA may also be derived from other fungal material such as hyphae and tissue fragments. Although it is generally assumed that spores comprise the majority of airborne
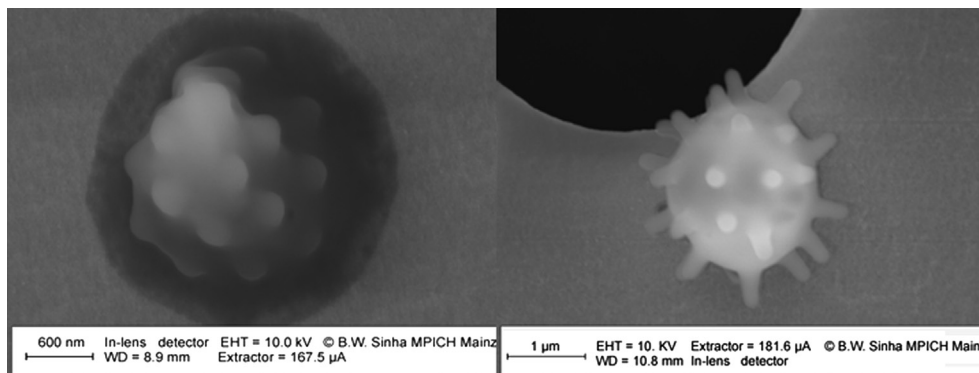

Fig. 3.   Fungal spores with and without coating by secondary organic aerosol (dark gray envelope in left panel). Electron micrographs of aerosol filter samples from pristine tropical rainforest air in the Amazon (Pöschl et al., 2010), (Reproduced with permission from AAAS).

fungal material, this remains largely unsubstantiated and has important implications for interpretation of both, laboratory or field measurements. Hyphal fragments have been observed in ambient air in a number of studies (Gorny et al., 2002; Green et al., 2006). Sinha and Kramer (1971) suggested that airborne hyphae are most commonly unbranched conidiophores that can be 1–100 μm in length but that are more commonly 5–40 μm. Pady and Gregory (1963) summarise the observed concentrations to be within the range 10^0–10^3 m^{-3} and observed that a large fraction of ambient hyphae were viable and able to germinate resulting in fungal colony growth. As most fungal species in the biosphere are still unknown, the detection and characterisation of fungi in atmospheric aerosol samples by DNA analysis can help to elucidate the global spread and diversity of fungi. As a by-product of the active emission process, fungal spores can be coated with specific sugar (e.g. arabitol, mannitol) and sterol (e.g. ergosterol) compounds that have thus been utilised as chemical tracers for ambient fungal spore concentrations (Lau et al., 2006;

Bauer et al., 2007). Spores can also be coated with hydrophobin compounds that may affect both, their ice-nucleating ability (Iannone et al., 2011) and the immune response they cause after human inhalation (Aimanianda et al., 2009).

Depending on biological species, age and ambient conditions, the diameter of fungal spores can vary ($\sim$1–50 μm); most frequently it is in the range of 2–10 μm (Elbert et al., 2007; Wang et al., 2008; Fröhlich-Nowoisky et al., 2009; Huffman et al., 2010). Furthermore, fungal spores are often observed to aggregate into long chains of spores that greatly affect their aerodynamic diameter and have implications for both, atmospheric lifetime and deposition into human tissues (Lacey, 1991; Reponen et al., 2001).

The number and mass concentrations of fungal spores are typically observed to be $\sim$10^4 m^{-3} and $\sim$1 μg m^{-3}, respectively, in continental boundary layer air (Tables 3 and 4). They account for up to $\sim$10% of organic carbon (OC) and $\sim$5% of PM$_{10}$ at urban and suburban locations

Table 3. Global emission estimates for different types of PBAP and size ranges of air particulate matter (PMx, x = upper limit of particle diameter; TSP = total suspended particulates)

	Global emissions (Tg yr^{-1})	Size range	References
Bacteria	0.74 (0.4–1.8)	Diameter: 1 μm (PM$_1$)	Burrows et al. (2009b)
	0.7	Diameter: 1 μm (PM$_1$)	Hoose et al. (2010a)
	2.58	Diameter: 1.17 μm	A. Sesartic, personal communication
	28.1	Lognormally distributed with geometric mean number diameter: 2 μm, standard deviation = 1.37	Jacobson and Streets (2009)
Fungal spores	8	Diameter: 4 μm (PM$_4$)	Sesartic and Dallafior (2011)
	28	Two size modes: fine (<2.5 μm) and coarse (2.5–10 μm) (PM$_{10}$)	Heald and Spracklen, (2009)
	31	Diameter: 5 μm (PM$_5$)	Hoose et al. (2010a)
	50	Diameter: 5 μm (PM$_5$)	Elbert et al. (2007)
	186	Lognormally distributed with geometric mean number diameter: 3 μm, standard deviation = 1.37	Jacobson and Streets (2009)
Pollen	47	Diameter: 30 μm (PM$_{30}$)	Hoose et al. (2010a)
	84	Lognormally distributed with geometric mean number diameter: 30 μm, standard deviation = 1.37	Jacobson and Streets (2009)
Total PBAP	<10 (dominated by plant debris and fungal spores),	Diameter: 4 μm for fungal spores; diameter not specified for plant debris (TSP)	Winiwarter et al. (2009)
	56 (0–90)	Diameter <2.5 μm (PM$_{2.5}$)	Penner (1995)
	78 (includes only bacteria, fungal spores and pollen)	Diameters as above (PM$_{30}$)	Hoose et al. (2010a)
	186	Split equally into the two coarse size fractions: 2.5–5 and 5–10 μm (PM$_{10}$)	Mahowald et al. (2008)
	296 (includes only bacteria, fungal spores and pollen)	Diameters as above	Jacobson and Streets, (2009)
	$\sim$1000 (includes cellular fragments)	TSP	Jaenicke (2005)

Table 4. Characteristic magnitudes of the number and mass concentrations of PBAP in air over vegetated regions

	Number concentration [m^{-3} air]	Mass concentration [µg m^{-3}]	Size range	References
Bacteria	∼10^4	∼0.1	PM$_{10}$	Bauer et al. (2002a); Burrows et al. (2009a)
Plant debris (free cellulose)		∼0.1–1	PM$_{10}$	Sánchez-Ochoa et al. (2007)
Viral particles	∼10^4	∼10^{-3}		This work, Sect. 2.4
Fungal spores	∼10^3–10^4	∼0.1–1	TSP	Elbert et al. (2007); Fröhlich-Nowoisky et al. (2009)
Fungal hyphal fragments	∼10^3			Pady and Gregory (1963)
Pollen	∼10 (up to ∼10^3)	∼1	TSP	Sofiev et al. (2006); Fröhlich-Nowoisky et al. (2009)
Algae	∼100 (up to ∼10^3)	∼10^{-3}		Reisser (2002)
Fern spores	∼10 (up to ∼10^3)	∼1	TSP	Mücke and Lemmen (2008)

(Bauer et al., 2002a, 2000b, 2008a). In pristine tropical rainforest air, fungal spores account for up to ∼45% of coarse particulate matter. Thus, the properties and effects of fungal spores may be particularly important in tropical regions where both, physico-chemical processes in the atmosphere and biological activity at the Earth's surface are particularly intense (Graham et al., 2003; Gilbert, 2005; Elbert et al., 2007; Pöschl et al., 2010; Zhang et al., 2010), but chemical tracers typical of fungal spores have also been reported in aerosols from semi-arid and arid sites (Graham et al., 2004).

Most airborne fungi belong to the divisions of *Ascomycota* and *Basidiomycota* (Fröhlich-Nowoisky et al., 2009). Most *Ascomycota* and *Basidiomycota* actively eject their spores with liquid jets or droplets (osmotic pressure and surface tension effects), whereas others rely on dry spore detachment by wind or other external forces. Dry-discharged spore concentrations tend to be enhanced during warm, dry weather conditions, whereas actively wet discharged spores tend to be enhanced during humid conditions such as those at night and in the early morning hours (Graham et al., 2003; Elbert et al., 2007). Emission and dispersal of fungal spores can thus be selectively correlated with various meteorological parameters and usually have specific behaviours, depending on the species involved (Fitt et al., 1989; Pasanen et al., 1991; Calderon et al., 1995; Katial et al., 1997; Sabariego et al., 2000; Troutt and Levetin, 2001; Burch and Leventin, 2002; Jones and Harrison, 2004; Grinn-Gofron and Mika, 2008; Oliviera et al., 2009).

From spore counts and molecular tracers, Elbert et al. (2007) derived a global emission rate of ∼50 Tg a^{-1} for fungal spores, corresponding to average mass and number emission fluxes of ∼23 ng m^{-2} s^{-1} and 200 m^{-2} s^{-1}, respectively, over land. These values are in fair agreement with the global average model estimates of Heald and Spracklen (2009): ∼28 Tg a^{-1} or ∼6 ng m^{-2} s^{-1} over land, and 189 Tg a^{-1} calculated by Jacobson and Streets (2009) for the year 2000. For Europe, Winiwater et al. (2009) derived a value of ∼0.6 ng m^{-2} s^{-1}, and recently

Sesartic and Dallafior (2011) estimated average mass and number flux values of ∼17 ng m^{-2} s^{-1} and 513 m^{-2} s^{-1} over land. Overall, the studies indicate that the global average emission rates of fungal spores are uncertain by about one order of magnitude, which appears comparable to many aerosol sources and less than for other types of PBAP (Table 3). More field data are required to constrain better the actual emission flux of fungal spores on regional and global scales.

Studies based on DNA obtained directly from atmospheric aerosol samples offer new possibilities to identify the origin of fungal matter, independent of viability, cultivability and fragmentation (e.g. Boreson et al., 2004; Peccia and Hernandez, 2006; Fierer et al., 2008; Bowers et al., 2009; Fröhlich-Nowoisky et al., 2009). DNA-based techniques can amplify target regions of the DNA extracted directly from atmospheric aerosol samples. Amplification of the internal transcribed spacer (ITS) regions between the 18S and 28S ribosomal ribonucleic acid (rRNA) genes provides good target regions to identify fungi to genus and often to species level (O'Brien et al., 2005; Fröhlich-Nowoisky et al., 2009). DNA sequencing of this region has proven to be an efficient tool for the detection of rare and hard-to-cultivate fungi (e.g. *Blumeria graminis*) as well as highly abundant and easy-to-cultivate fungi (e.g. *Cladosporium sp.*) in aerosol samples (Fröhlich-Nowoisky et al., 2009) and other habitats (e.g. Hunt et al., 2004; O'Brien et al., 2005).

With regard to species richness, Fröhlich-Nowoisky et al. (2009) detected 64% *Basidiomycota* and 34% *Ascomycota* in a semi-urban environment in central Europe, whereas Bowers et al. (2009) found only 4% *Basidiomycota* but 82–92% *Ascomycota* at a mountain site in North America. On the class level within the *Ascomycota, Dothideomycetes* and *Eurotiomycetes* seem to be the prevalent groups (Bowers et al., 2009; Fröhlich-Nowoisky et al., 2009). These findings may be influenced not only by regional differences but also by measurement issues, and the actual biogeographic distribution of airborne fungal species is a subject of

ongoing studies (Womack et al., 2010; Fröhlich-Nowoisky et al., 2011). As in bacteria, seasonal variation exists and differs between sampling sites also for fungi. During hot summer seasons, a decrease in the airborne microflora was reported for some fungi (Mullius et al., 1984; Filipello-Marchision et al., 1992; Fröhlich-Nowoisky et al., 2011).

The detection and apparent frequency of occurrence of different species can be affected by technical factors such as extraction efficiency of genomic DNA, varying rRNA gene copy number in the species, primer matching and performance, amplification efficiency of the target region, and cloning success. To our knowledge, from the few studies that have reported DNA analyses of fungi in atmospheric aerosol samples, some had neither found the expected high abundance of, e.g. *Cladosporium* sp. nor a high species richness (in particular *Basidiomycota*), which may well be due to limitations of the applied PCR primers (e.g. Després et al., 2007; Fierer et al., 2008; Bowers et al., 2009), although over 1500 fungal DNA sequences from 5 urban air samples were measured by Fierer et al. (2008) and several dozens of filter samples of urban, rural and high-alpine air were analysed by Després et al. (2007). Thus, careful selection and combination of multiple PCR primer pairs and other materials for the extraction and amplification of DNA obtained from aerosol samples are key elements for achieving high coverage of species richness (>300 species), as discussed in Fröhlich-Nowoisky et al. (2009). The high number of fungal species that were detected only once indicates that a higher number of samples and clones would have to be investigated for a complete coverage of species diversity (Fröhlich-Nowoisky et al., 2009). In any case, the detected and reported numbers and frequencies of occurrence of species, families and classes can only be taken as a lower limit for the actual diversity and frequencies of occurrence.

2.3. Pollen

Among PBAP types, pollen grains can be among the largest in physical size and represent the reproductive units of plants that contain the male gamete. Pollen grains vary in size between 10 and 100 μm, have various shapes and have a hard shell that protects the sperm cells during the transportation processes. Pollen grains occur as biological aerosols not only as complete units but also as fragmented pieces. Pollen can rupture when the humidity is high, and these fragments have been shown to be in the range from 30 nm to 5 μm (Taylor et al., 2002, 2004; Miguel et al., 2006). Pollen of anemophilous plants use wind as their dispersal vector and have a typical diameter of 17–58 μm (Stanley and Linskins, 1974; Kuparinen, 2006; Nathan et al., 2008; Pope, 2010). They are usually dispersed in large amounts and over wide ranges because of their floating ability (Straka, 1975). The pollen is often ejected in clumps that stick to their neighbouring vegetation and are blown away after drying (Jones and Harrison, 2004).

The ability of pollen to disperse into the atmosphere depends on several parameters. On the one hand, dispersal depends on resuspension as described in detail by Jones and Harrison (2004). On the other hand, pollen dispersal depends on meteorological factors. For example, bonding of pollen to surfaces is affected by temperature and moisture and thus by temperature and humidity of the air (Jones and Harrison, 2004). It has also been shown that pollen counts in, for example, the cypress family show significant positive correlations with daily minimum, mean and maximum temperatures and negative correlations with precipitation (Lo and Levetin, 2007). After temperature and humidity, wind and rain are typically the most important parameters for pollen dispersal, and it has been shown that pollen emission is reduced in the presence of rain or when the wind speed was low (Ogden et al., 1969). In general, the pollen concentration decreases with height, and for birch it could be shown that at 2000 m just 40% of the ground concentration were present (Rempe, 1937). This general phenomenon can be modified by inversion layers (Linskens and Jorge, 1986). The horizontal distance over which pollen can be carried with the wind can depend on prevailing temperatures, and it has been suggested that an increase in air temperature may induce atmospheric instability and thus promote pollen dispersal (Kuparinen et al., 2009). However, pollen has been observed to be lifted into the upper layers of the atmosphere by convection (Monin and Obukhov, 1954; Tackenberg, 2003; Taylor and Jonsson, 2004; Wright et al., 2008), and this ability makes pollen grains possibly relevant as ice nuclei in many environments.

The residence time of pollen in the atmosphere depends on their settling velocities that depend on morphology (shape), density and size of the pollen and vary widely among pollen types (Digiovanni et al., 1995; Diehl et al., 2001). The time pollen stay aloft in the atmosphere also influences the horizontal distance they can travel. Long distance dispersal (LDD) is not only interesting from the atmospheric point of view but also shapes many fundamental processes in plant ecology and evolution (Ellstrand, 1992; Kawecki and Ebert, 2004; Neilson et al., 2005; Nathan et al., 2008), e.g. the ability of plants to spread into new areas (IPCC 2007a). Dust is well known to frequently travel long distances, even across oceans (Kellogg and Griffin, 2006; Ben-Ami et al., 2010). Biological particles can also be transported over similar distances and have been observed to accompany dust plumes thousands of miles from their assumed sources (Shinn et al., 2000; Kellogg and Griffin, 2006; Polymenakou et al., 2008; Hallar et al., 2011). The LDD of wind-dispersed pollen is

typically promoted by turbulent vertical fluctuations in wind and by coherency in vertical eddy motion that uplifts seeds well above the vegetation canopy (Nathan et al., 2002; Tackenberg, 2003; Soons et al., 2004). For a wide range of plant types, a positive relationship has been observed between mean air temperature and the frequency of LDD by wind in a boreal forest. Thus, an increase in local air temperature increases pollen dispersal distances (Kuparinen et al., 2009).

Another characteristic of pollen is their seasonality, as the presence of pollen in the atmosphere follows a clear seasonal cycle in response to the flowering seasons of the plant sources (Tormo et al., 2010). On a local scale, the pollination season for each plant is predictable and only shifts slightly as a function of meteorological parameters. The amount of pollen disposed by individual plants can vary greatly from 1 yr to another. Pollination during a given season always has a date, at which the pollen begins to disperse but at lower numbers, followed by the main pollination season when most of the pollen is dispersed, and conclude by a date when the plant stops its pollen-producing phase. However, usage of this nomenclature varies greatly within the literature and can be confusing (Jato et al., 2006). In addition, sedimented pollen might be resuspended again from dry surfaces. Pollen grains occasionally show a diurnal cycle with concentrations rising 1–2 h after dawn, peaking a few hours later and decreasing through the afternoon (Jones and Harrison, 2004). The phenomenon of diurnal variability is also common among other biological aerosol types such as bacteria and fungal spores (Jones and Harrison, 2004; Huffman et al., 2010).

Pollen grains are large PBA particles that typically lead to short atmospheric residence times. However, they can be up-drafted to high altitudes and have large residence times, and thus pollen can reach concentrations comparable to ice nuclei in some circumstances (Scheppegrell, 1924; Pruppacher and Klett, 1997; Diehl et al., 2001). Detailed information on the behaviour of pollen in ice nucleation is given in section 4.2.

Global changes, such as increasing atmospheric CO_2 concentrations, increasing temperature, changes in the amount, distribution, and intensity of precipitation events, increases in the intensity and frequency of certain extreme weather events, changes in land use, and urbanisation, will likely have an impact on the production, distribution and dispersion of pollen (IPCC 2007b; Reid and Gamble, 2009). Climatic changes may lead to shifted or even elongated pollinations seasons. As pollen is known to cause allergies in humans, these shifts may also lead to changes in human exposure and changes in the prevalence and severity of symptoms in individuals with allergic diseases (Reid and Gamble, 2009). Alterations in the timing of aeroallergen production in response to weather variables

have been clearly demonstrated for certain tree species, but less for grass, weed and mould (Katial et al., 1997; Emberlin et al., 2002; Clot, 2003).

Because pollen allergies can cause such medical problems, various pollen-monitoring programmes, networks and databases have been developed recently to provide data on pollen observation, share methods, encourage collaborations and thus create foundation for intensive pollen research. Examples include the Pollen Monitoring Program in Europe (Giesecke et al., 2010) and the Pollen Biology Research Coordination Network in the United States. The Global Pollen Database combines pollen information from Africa, the Americas and northern Asia made available by regional networks such as the Indo Pacific Database, the Latin America Pollen Database and the North American Pollen Database. These international collaborations are helping to advance knowledge of global pollen distribution.

In addition to climate-related changes in the atmospheric abundance of pollen and fungal spores, the allergenic potential of PBAP can also be enhanced by interactions with air pollutants (Taylor et al., 2002; Franze et al., 2003; Taylor and Jonsson, 2004; Franze et al., 2005; Pöschl, 2005; Reid and Gamble, 2009). For example, the reaction with ozone and nitrogen oxides leads to the formation of reactive oxygen intermediates and nitrated proteins that can influence the interaction of PBAP with the immune system and trigger or exacerbate allergic diseases (Gruijthuijsen et al., 2006; Shiraiwa et al., 2011; Zhang et al., 2011).

2.4. Viruses

Viruses are among the smallest of common PBAP classes, with physical diameter as low as 20 nm (Dongsheng, 2006). However, viruses are not commonly airborne as individuals and are more likely attached to other suspended particles (e.g. Yang et al., 2011).

Many diseases present in humans, animals, birds, fish, insects and plants are caused by viruses found in aerosols (one of possible routes of infection transmission), confirmed by numerous laboratory studies (Akers, 1969; Akers, 1973; Verreault et al., 2008). However, publications revealing the presence of viruses as PBAP are not numerous (Gloster et al., 1982; Christensen et al., 1990; Grant et al., 1994; Chen et al., 2008b). This perceived lack of research might be connected to the fact that before the development of molecular biological methods (e.g. PCR) to detect genetic material of microorganisms (Alvarez et al., 1995; Peccia and Hernandez, 2006), only viable viruses could be found in air samples. There are no universal test systems for virus detection such as nutrient media for bacteria or fungi. Instead, sensitive cell cultures, embryo-

nated chicken eggs or susceptible laboratory animals are required (Zhdanov and Gaudamovich, 1982a; Zhdanov and Gaudamovich, 1982b), and specific test systems allow only the detection of viruses replicating in them. No other viable viruses, which can also be present in aerosol samples, will be detected.

Another possible reason for the scarcity of publications containing information on viable viruses in atmospheric aerosol is inactivation of viruses in the atmosphere under the influence of different environmental factors (changes in temperature, relative humidity, solar radiation, etc.). Unlike bacteria, fungi and algae, viruses have no repair systems, and therefore, their inactivation rates are usually higher than those of living microorganisms.

According to Posada et al. (2010), the inactivation rate of viruses in an aerosol can be described by:

$$C/C_0 = e^{-kt}$$

Here C is the concentration of viable viruses at the time t, C_0 is the initial concentration of viable viruses and k is the rate coefficient of inactivation. Even for the most stable viruses, k is typically of the order of 0.01 min^{-1}, corresponding to an effective half-life of about one hour (Donaldson, 1973; McDevitt et al., 2008). For most other viruses, the inactivation rate in aerosol is considerably higher (Harper, 1961; Miller et al., 1963; de Jong, 1965; Miller and Artenstein, 1967; Songer, 1967; Akers, 1969; Benbough, 1971; Barlow, 1972; Donaldson, 1972; Akers, 1973; Donaldson and Ferris, 1974). Viruses are almost completely inactivated in aerosols in the span of 1 d under such conditions.

Experimental data on the survival of viruses show that, on the whole, the inactivation rate becomes higher for all viruses with increasing temperature (Zhdanov and Gauda-movich, 1982a; Zhdanov and Gaudamovich, 1982b; Weber and Stilianakis, 2008). Also, the number of surviving viral particles in aerosol decreases with increased radiation dose that the virus aerosol is exposed to (Jensen, 1964; Zhdanov and Gaudamovich, 1982a; Zhdanov and Gaudamovich, 1982b; Sagripanti and Lytle, 2007; McDevitt et al., 2008). Relative humidity influences the survival of viruses in aerosol differently. For example, the survival rate of influenza virus in aerosol is highest at high relative humidity, whereas that of foot-and-mouth disease virus is highest at intermediate relative humidity (50–60%) (Akers, 1969; Donaldson, 1972; Schaffer et al., 1976; Weber and Stilianakis, 2008).

The use of molecular biological methods for detecting genetic material of viruses also involves certain difficulties. As genetic material of different viruses is presented by very different variants: DNA or RNA (ribonucleic acid) mole-cules, single-stranded genomes (with + or − strand), frag-

mented genomes, etc. (Zhdanov and Gaudamovich, 1982a), no universal PCR primer for detection of all viruses has been developed so far. Consequently, such methods determine only the presence of expected viruses in samples. For example, Chen et al. (2008c) presented the results of search for different subtypes of influenza-A virus in the atmosphere of Taiwan. Other viruses in atmospheric air samples were not even sought.

Virus-containing aerosols are formed in spray from water surfaces (Baylor et al., 1977a; Baylor et al., 1977b; Baylor and Baylor, 1980), from aerosolised virus-destroyed tissues of plants, insects, animals and birds; they are also shed by sick animals, birds and humans (Zhdanov and Gaudamovich, 1982b; Jones and Harrison, 2004). One should also note the intentional use of aerosols of insect viruses for plant protection (Morris, 1980; Maiorov et al., 1985; Jinn et al., 2009). The transfer of virus-containing aerosols in the atmosphere has been described for local scales, e.g. near sludge wastewater treatment plants and stock farms (Strauch and Ballarini, 1994; Carducci et al., 1995; Sigari et al., 2006; Langley and Morrow, 2010) as well as for regional scales, e.g. transfer of foot-and-mouth disease virus across the English Channel (Gloster et al., 1982) and transfer of avian influenza virus from continental China to Taiwan (Chen et al., 2008b). The hypothesis of transcontinental transfer of influenza A virus aerosol was demonstrated by Hammond et al. (1989). Consequently, virus-containing aerosols can spread worldwide.

Relatively few studies have attempted to comprehensively estimate the concentration of different viruses in ambient air and evaluate their source strength. One example of such a study was reported by Safatov et al. (2010) who collected 30 samples of atmospheric air (10–15 m^3 each) onto fibrous filters during different seasons in Southwestern Siberia. Samples were analysed using the PCR method for the presence of viruses known to cause respiratory diseases, although no virus genetic material was found. It should be noted, however, that Southwestern Siberia is not endemic to airborne viral infections largely because it is located far from sources of viruses such as influenza (Chen et al., 2008c) and habitats of migrant birds transmitting influenza viruses (Liu et al., 2005). Electron microscopy during the same study detected bacteria, fungal spores and plant fragments (Safatov et al., 2010), but virus-like particles are impossible to confidently detect without genetic methods such as PCR, as discussed above.

As noted by Chen et al. (2008b), the total concentration of different subtypes of influenza A viruses can reach 800 m^{-3} copies of genetic material of these viruses in the ambient atmosphere of Taiwan and up to $3 \cdot 10^4$ m^{-3} in outdoor pet markets in Taiwan. It should be noted that Taiwan, like the whole of South-East Asia, is an endemic area for this virus, which explains the higher influenza virus

concentrations in this region. For other viruses originating from local sources, such as excreta of infected animals and humans, sewage treatment plants, use in agriculture, etc. (Fannin et al., 1985; Carducci et al., 1995; Sigari et al., 2006), the total numbers of viruses in aerosol are not large, and their contribution to the total mass of aerosol is negligible. As for more powerful sources, such as soil, vegetation and water surfaces, data on virus aerosol in the air in natural conditions are available only for the latter (Baylor et al., 1977a, 1977b; Baylor and Baylor, 1980). Virus-like particles can also be present in the atmosphere and water, such as those described by Leck and Bigg (2005a) using electron microscopy. The concentration of virus-containing particles in the air is low, however (less than 100 cm^{-3} – total concentration of aerosol particles with diameter larger than 90 nm in marine atmosphere; data from Bigg et al. (1995)), and by these methods it is impossible to distinguish viruses from particles on which they are bounded.

Virus aerosols collected from the exhaled air of infected animals have been the subject of various research studies. For example, for pigs infected with classical swine fever virus, the concentration of viral particles may reach 10^4 m^{-3} of air (Weesendorp et al., 2008). Other infections of animals and birds (such as foot-and-mouth disease, Newcastle disease, etc.) are characterised by virus aerosol exhalation of the same order of magnitude (Downie et al., 1965; Donaldson et al., 1983; Donaldson and Alexandersen, 2002; Li et al., 2009). Taking into account that the number of infected animals is typically not large, the total number of exhaled viruses in aerosol is similarly small.

To evaluate the total mass of viruses in 1 m^3 of the atmosphere, let us consider an upper limit to the ambient concentration of viral particles to be $3 \cdot 10^4 \text{ m}^{-3}$. Assuming a per virus mass of $2 \cdot 10^{-17}$ kg, one of the heaviest known viruses (vaccina virus, Zhdanov and Gaudamovich, 1982b) yields an estimated virus mass concentration of $6 \cdot 10^{-4} \text{ µg m}^{-3}$. This estimate is approximately four orders of magnitude smaller than the total concentration of biogenic substance in the atmosphere (Jaenicke, 2005; Table 4) and thus, even if the concentration of viruses in the atmosphere was underestimated by an order of magnitude, the average mass concentration of viruses in atmospheric air would be very small compared to other biogenic aerosol mass.

2.5. Algae and cyanobacteria

The occurrence of algae in fresh and sea water is well known. However, algae living outside of the aqueous environment rarely attract attention. These algae are termed terrestrial, aeroterrestrial, aerophytic or subaerial, are able to reside on almost all substrates, natural or artificial and can become airborne, constituting the aero-(phyto) plankton. Chlorophycean and xanthophycean species are common worldwide (Printz, 1921; Laundon, 1985; Dubovik, 2002; Reisser, 2002; Sharma et al., 2007; Neustupa and Skaloud, 2010) and exist free living as well as lichenised (Bubrick et al., 1984). Due to the size of the algae and their spores, many smaller than 10 µm in diameter (Printz, 1921; Dubovik, 2002; Burchardt and Dankowska, 2003; Neustupa and Skaloud, 2010), they can be easily dispersed in the atmosphere. In a recent review article, the mechanisms involved in the aerosolisation of algae were presented, and Sharma et al. (2007) stated that 'airborne algae are the least-studied organisms in both aerobiological and phycological studies'. This seems to be valid for aerosol studies, too. Quantitative measurements of algae in ambient air are very rare and it was reported (Reisser, 2002) that algal cells are present at a concentration of 300–500 cells m^{-3} of air on a dry and sunny summer day (Table 4).

Cyanobacteria belong taxonomically to bacteria, although they have long been considered as algae, as they have the ability to obtain their energy through photosynthesis. Due to their colour, they have been called blue-green algae, but they still belong – as they lack a cell nucleus – to the bacteria domain. As cyanobacteria can be found in almost every environment, have habitats across all latitudes, are widespread in oceans and freshwater, terrestrial ecosystems and bare rock and soils as well as in extreme habitats such as hot springs, they have been considered to be one of the most successful groups of microorganisms. They fulfil vital ecological functions in the world's oceans as important contributors to global carbon and nitrogen budgets (Stewart and Falconer, 2008). Cyanobacteria can not only occur as planktonic cells but also create biofilms in marine, freshwater and terrestrial environments. A few are involved in symbiosis with lichen, plants and other organisms and provide energy for their host. Although well studied in the marine environment, not much is known about their presence in the atmospheric environment.

Airborne cyanobacteria were found in Varanasi City, India, where they were more abundant than green algae and diatoms; *Phormidium fragile* as well as *Nostoc muscorum* were recorded throughout the 2 yr of sampling (Sharma and Rai, 2008). Similar observations were made in Cairo, Egypt. The species *Chroococcus limenticus*, *Lyngbya lagerheimii* and *Schizothrix purpurascens* appeared in all seasons (El-Gamal, 2008). Genitsari et al. (2011) recently published an overview of taxa of airborne algae and cyanobacteria found in aerobiological studies.

2.6. Biological crusts and lichens

Arid and semi-arid regions of the globe exhibit biological crusts (also called rock varnish, cryptobiotic, microbiotic or biological soil crust) consisting of bacteria, fungi, algae, lichens and bryophytes in variable proportions (Belnap et al., 2003). Rock varnishes are natural, thin (5 μm – 1 mm), brown, black or grey (lead colour) coatings on rock surfaces (Krumbein and Jens, 1981). They consist largely of iron and manganese oxides with some quartz, clays and carbonates admixed. They may contain considerable amounts of organic material that sometimes may be responsible for the gel-like or lacquer-like appearance. The grey or black films may sometimes consist predominantly of dry cyanobacteria. Rocks outside of deserts often are also covered by a varnish (Douglas, 1987). Although these rock crusts are not suspended into the air by active mechanisms, they can be eroded from their host surface and broken into fragments producing small dust particles (Grini et al., 2002; Büdel et al., 2004). Parts of biological soil crusts can also be ablated from desert surfaces, and all these particles may contribute to the content of organic material in dust transported over long distances during storms (Grini et al., 2002; Büdel et al., 2004; Prospero et al., 2005; Hua et al., 2007).

As lichens are a symbiotic form of life between a wide range of fungi, algae or cyanobacteria (Hawksworth et al., 1995; Nash III, 1996) and distribute separately or together via the air, they also can, in certain circumstances, constitute a subgroup of PBAP. As biological aerosols, they may play a role in ice nuclei activity as well as in health effects. Lichen, for example, can cause human allergenic reactions (Richardson, 1975; Fahselt, 1994; Ingolfsdottir, 2002).

Although lichens are regarded as an individual taxonomic group – lichen taxonomy is based on the taxonomy of the fungal partner, the mycobiont (Tehler, 1996) – they also must be considered separately from their host because lichens are different in behaviour and life form from their isolated partners (Nash III, 1996; Tehler, 1996). Nearly 20% of all known fungi species are lichenised (Lutzoni et al., 2001) and more than 98% of the lichenised fungi belong to *Ascomycota* and a few to *Basidiomycota* (Hawksworth et al., 1995; Tehler, 1996). Most of the lichenised fungi form symbioses with *Chlorophyta*, whereas only about 10% lichenise with cyanobacteria and 3% with both (Tschermal-Woess, 1988; Lewis and McCourt, 2004).

In general, lichens can be found in three major life forms that all can contribute to biological aerosol particles: a crust-like biofilm (crustose), a leaf-like (foliose) and a branched tree-like biofilm (fruticose) as described in Hawksworth et al. (1995) and Büdel and Scheidegger (1996). Especially for PBAP formation, the presence of lichens in extreme habitats is interesting. They can deal with extreme light, dryness or temperature that are less favourable for higher plants. They are also tolerant to extreme desiccation and UV light exposure due to their cortical pigments (Nybakken et al., 2004; Gauslaa, 2005; Vráblíkova et al., 2006). Their ability to prevent the formation or to scavenge free radicals also increases their chance of surviving during their transport in air. Lichens face considerable problems in colonising new sites and maintaining existing populations. Mycobionts can distribute separately via Asco- or Basidiospores, or asexual by singular lichen structures, that contain both, mycobiont and phycobiont, such as insidia (protuberances from the thallus of corticated algae and medullary tissue), soredia (several algal cells encased by a hyphae) or hormocrusts (fragments if filamentous cyanophyte *Nostoc spp* with hypha penetrating the thallus fragments (Marshall, 1996; Oksanen, 2006)).

Although lichen species have been detected in the atmosphere, estimates of lichens biomass and consequently estimates of the number of lichen-derived aerosol particles are difficult. Lichen species are adapted to almost every temperate to extreme environment on Earth, such as arctic tundra, hot deserts, rocky coasts, or toxic slag heaps, but the spread of lichen population within each environment type is different. They are abundant on plant leaves or branches in rain forests or temperate woodlands, as well as on bare rock including walls, and on exposed soil surfaces. Henderson-Begg et al. (2009) suggested that canopy lichen biomass in temperate forest is similar to leaf biomass. Lichen detection directly in air has been pursued by Marshall (1996) in an aerobiological monitoring programme, where he found lichen soredia to be the most abundant airborne propagule with a size range of 30–100 μm on Signy Island in Maritime Antarctica.

Lichens are not only adapted to survive hot and dry environmental conditions but are also often frost tolerant (Kershaw, 1985). In ice nucleation studies pursued by Kieft (1988), nearly all lichens tested showed ice nucleation activity at temperatures above $-8\,°C$ or even above $-5\,°C$ (see also Table 6). In theory, the IN could be the bacterium or the fungal partner, but the failure to culture IN bacteria from lichen and also the high density of IN in active lichen carrying only few numbers of bacteria suggests a non-bacterial source of lichen IN. Studies by Kieft and Ahmadjian (1989) show that in their tests, always the mycobiont was responsible for IN activity. IN activity in lichen might enhance the uptake of atmospheric moisture by enhancing the condensation or causing deposition of ice from water vapour. Lichen-associated IN might even contribute to atmospheric IN (Kieft, 1988).

2.7. Others

Apart from the PBAP defined above, there exist a variety of other primary aerosol particles from the biosphere. Plant fragments, in particular, are one of the largest mass fractions of atmospheric PBAP and comprise a wide spectrum of decaying matter. However, drawing a consistent definition between PBAP and other organic matter can be difficult because plant materials can eventually be broken down into humic-like substances (HULIS, Fuzzi et al., 2006; Graber and Rudich, 2006) by oxidative modification and degradation of biopolymers, and are therefore, important components of soil. Cellulose, a homopolymer of D-glucose (Pöhlker et al., 2011), is the most frequently occurring biopolymer in the terrestrial environment (Butler and Bailey, 1973; Sánchez-Ochoa et al., 2007), although other biopolymers and structural components (e.g. lignin, chitin) may also be atmospherically relevant (Pöhlker et al., 2011). Cellulose is a major component of plant tissue and pollen and can be produced by some bacteria (Cannon and Anderson, 1991) but is not present in insects and animalian tissue (Winiwarter et al., 2009). Atmospheric concentrations of cellulose thus exhibit a strongly seasonal cycle and have been shown to have mass concentrations at least in the order of $\sim 0.5 \ \mu g \ m^{-3}$ (Puxbaum and Tenze-Kunit, 2003). Presence of cellulose in atmospheric aerosols has also been frequently used as a proxy for total concentrations of plant debris (e.g. Sánchez-Ochoa et al., 2007; Winiwarter et al., 2009). Due to large particles of biological material being lifted into the atmosphere (e.g. air-dispersed seeds), the actual concentration of cellulose and related materials in total air particulate matter may be substantially higher under windy conditions.

Emissions of liquid and solid secretions from organisms are also found in the atmosphere. Brochosomes and epicuticular wax (Wittmaack, 2005; Wittmaack et al., 2005) are expelled from leafhoppers and do not contain cells. Brochosomes serve as a highly water-repellent body coating of leafhoppers. They usually become airborne not as individuals but in the form of large clusters containing up to 10 000 individuals or even more, but then usually separate into individual brochosomes or small clusters. They are extremely widespread and can be found in aerosol samples from all continental regions (Bigg, 2003). Exopolymer secretions (EPS) of microalgae and bacteria in water become airborne with the bubble-bursting mechanism (Leck and Bigg, 2005a, 2005b). EPS might deteriorate the ability of sea spray particles acting as Cloud condensation nuclei (CCN, see studies in Section 4.1).

Other sources of PBAP are fur fibres, dandruffs and skin fragments of animals (including humans) that are shed in large amounts per day and can also be airborne (Cox and Clark, 1973). Insect fragments have also been observed in a number of studies and thus may represent an important class of physically large PBAP in some areas (e.g. Wittmaack, 2005). Whole macroscopic organisms, such as spiders lofted to air by silk 'ballooning' lines, have been observed to travel extremely long distances (>several 100 km) and to high altitudes (stratosphere) (e.g. Thomas et al., 2003). These organisms may contribute to PBAP dispersal efficiently through body or silk fragments.

2.8. Characteristic concentrations and emission estimates

Biological particles cover an extremely broad range of sizes and are morphological very diverse. Thus, measurements of ambient PBAP concentrations are extremely challenging and reports from literature have been very few. PBAP have unique properties, such as large particle size, cell viability concerns and physical changes associated with environmental variables (see Section 3.1). In addition, biological material suspended in the atmosphere undergoes drastic changes as a function of manifold biological variables such as species and ecosystem health, seasonal and episodic cycles and meteorology. As a result, average concentrations for PBAP are extremely difficult to estimate without rigorously taking all of these variables into account. However, PBAP concentrations have been estimated to be up to 25% of total aerosol mass on a global basis (Jaenicke, 2005), and so more detailed measurements are desperately needed.

As a first overview of global importance, Table 3 present a survey of global emission estimates and characteristic magnitudes for the number and mass concentration of major PBAP classes, respectively. Such synthesis provides means for discussion and motivation of future measurements.

3. Techniques for PBAP collection and analysis

3.1. PBAP sampling methods

The sampling and collection of atmospheric aerosols requires a sound understanding of the physical principles that govern interactions with suspended particles (<100 μm). As such, particle size is by far the most important characteristic for choosing a sampling procedure for both PBAP and all other classes of airborne particles (Nicholson, 1995). Losses of particles within inlets, inlet lines and instruments can cause huge biases in both quantitative and qualitative understanding, and therefore sampling procedures must be designed properly (Zimmermann et al., 1987). While small particles (<0.1 μm) are most susceptible to Brownian diffusion and electrostatic forces, large particles (>5 μm) are more influenced by losses due to

gravitational settling and inertial surface impaction. In addition, losses of particles to surfaces due to air turbulence can affect particles of all sizes. These issues are dealt with in detail elsewhere (e.g. Hinds, 1999; Baron and Willeke, 2001).

However, the sampling of biological aerosols often requires special handling procedures as compared to the sampling of inert particles and these are introduced briefly here. Although sampling issues due to particle size effects are not unique to biological aerosol sampling, PBAP size and mass are often hard to predict based on complicated relationships between the biological tissue and environmental variables such as temperature and relative humidity (e.g. Madelin and Johnson, 1992; Reponen et al., 1996). In addition, many biological particles (e.g. chain agglomerates of fungal spores) can have very elongated morphologies that can create large differences between physical and aerodynamic diameter measurements (Lacey, 1991; Reponen et al., 2001). Collection of living, or viable, material requires care in order not only to sample microorganisms appropriately but also to keep them alive until the desired analysis or cultivation can be performed. Certain species of bacteria and fungal spores are more easily cultivated than others, and in many cases this relates to the ability of sampled particles to survive harsh conditions related to sample collection (i.e. sun exposure, extended period of high airflow). Bacteria, in particular, are susceptible to damage or death when impacted too forcefully onto collection substrates (e.g. Stewart et al., 1995). Samples also must often be immediately frozen after collection to preserve DNA for later analysis. This can complicate sampling of PBAP in remote environments and add both uncertainty and bias to measurements. Small biological particles (e.g. viruses, bacteria) may also be attached to larger, non-biological particles such as mineral dust and thus be sized much larger than the microorganism by itself. This fact must be kept in mind when analysing size-resolved PBAP measurements. Due to the additional complexities in determining the biological nature of a collected set of particles compared to that of non-biological particles, PBAP measurements should be carefully scrutinised and in many circumstances taken as lower limit values.

As a result of the issues specific to biological aerosol sampling, a number of sampling methods have been developed primarily for PBAP collection. Again, a review of these topics can be found elsewhere (e.g. Henningson and Ahlberg, 1994; Madelin, 1994; Crook and Sherwood-Higham, 1997; Levetin, 2004; Xu et al., 2011) and so only a very brief overview of key classes of PBAP samplers will be given here. Devices that collect aerosol based on inertial forces have been particularly well utilised for PBAP measurement. The most common single-stage impactor

used for microbiological sampling has been the relatively simple slit-to-agar sampler (Henningson and Ahlberg, 1994), first developed by Bourdillon et al. (1941) and capable of providing CFU counts with high time resolution of approximately 1 h. Many different cascade impactors (multiple stages) have also been developed and extensively used for PBAP sampling (Mitchel, 1995). Probably, the most widely used of these has been the Andersen sampler (Andersen, 1958). This device has been frequently used as a reference method for sampling of culturable microorganisms, providing six or eight stages of particle sizing but due to physical constraints, the inner jets on each plate have a different sampling efficiency than the outer jets. An alternative in which this phenomenon is considered is the Berner-Impactor (Hillamo et al., 1991). The Marple 8-stage impactor is a personal cascade impactor design that provides size-resolved PBAP information directly from the breathing zone of an individual who wears it (Rubow et al., 1987). The Burkhardt spore trap has been an important sampler for collecting large PBAP such as fungal spores and pollen (Hirst, 1952). In it, air is brought in through a small slit in a housing designed to face the prevailing wind, and material collected continuously for up to a week can later be analysed via microscopy. Impingers collect airborne particles into liquid media and offer the possibilities of extended sampling times and increased collection efficiency with respect to many agar samplers (Crook, 1995a). Greenburg and Smith (1922) developed the first liquid impinger, and many types have since been designed for PBAP sampling (e.g. Henderson, 1952.). The AGI-30 has been particularly important and has been used as a reference sampler for the collection of viable organisms (Brachman et al., 1964; Henningson and Ahlberg, 1994). Other inertial samplers that have been commonly applied to PBAP collection include rotary arm samplers and both single- and multiple-stage centrifugal cyclones (e.g. IPCC 2007b; Crook, 1995a).

Non-inertial sampling methods such as passive settling and filtration have also both been widely used for PBAP collection. Many types of filter substrates have been used, including fibrous, flat (e.g. Nucleopore™) and membrane (Crook, 1995b). Each have their own advantages and disadvantages and these should be investigated thoroughly by the individual investigator. Electrostatic (Mainelis et al., 1999, 2002; Tan et al., 2011) and thermal precipitators (Kethley et al., 1952; Orr et al., 1956) have been developed in an attempt to collect viable aerosols with less damaging force. Recently, methods for online detection of biological aerosols have been developed using a variety of optical and additional techniques. These will be discussed in detail in Section 3.3.

3.2. Traditional analysis methods

Before the invention of molecular and other physicochemical methods, the diversity, identity and concentration of airborne microorganisms were primarily studied via microscopic analysis and cultivation methods on both selective and non-selective media. These methods have long and rich histories within aerobiological studies and still remain useful tools for PBAP analysis. Thus, the terms provided here ('traditional' and 'modern') are historical and somewhat arbitrary, but helpful for rough categorisation. A detailed discussion of these methods is beyond the scope of this text and can be found elsewhere (e.g. Cox and Wathes, 1995).

3.2.1. Cultivation.
Cultivation methods are only capable of collecting and detecting certain viable bacteria, fungi and algae, whereas they are incapable of detecting all other biological aerosol particles from these and other organism groups (e.g. dead bacteria and fungi, tissue fragments such as cell walls or cytoplasmic material). Although not capable of directly infecting a host, non-viable PBAP classes are still extremely important because they can provoke deleterious health effects (Gorny et al., 2002; Green et al., 2006) and may still be relevant for cloud formation.

As mentioned, studies investigating only the culturable fraction of PBAP have historically comprised a large portion of reported measurements. However, studies investigating cell viability suggest that the vast majority of environmental microbiota is non-culturable, even when viable (Staley and Konopka, 1985; Roszak and Colwell, 1987; Amann et al., 1995; Colwell, 2000; Rappé and Giovannoni, 2003; Wainwright et al., 2004b). Thus, studies based on culturing alone usually drastically underestimate microbial diversity (Fierer et al., 2008) and concentration. Only ~17% of known fungal species can be grown in culture (Bridge and Spooner, 2001) and for bacteria, the fraction is typically less than 10%, with an observed range of 0.01%–75%, and average values estimated at ~1% (Heidelberg et al., 1997; Lighthart, 2000; Chi and Li, 2007). In addition, the culturability of bacteria decreases rapidly following aerosolisation, (Heidelberg et al., 1997) and bacteria can be easily damaged when impacted via traditional sampling devices (Stewart et al., 1995). Within the culturing processes, additional biases may occur. For example, the sampling efficiency and culturability of viable bacteria depend strongly not only on the bacterial strain but also on experimental and environmental factors, including the growth medium used (ZoBell and Mathews, 1936; Kelly and Pady, 1954; Shahamat et al., 1997; Griffin et al., 2006), the choice of impaction versus filtration as a collection method (Stewart et al., 1995), the incubation

temperature and length of incubation time (Amato et al., 2007c; Wang et al., 2007; Wang et al., 2008), the air sampler volume (Griffin et al., 2006), relative humidity (Wang et al., 2001), time of day (Tong and Lighthart, 1999) and even the collection season (Amato et al., 2007c). Finally, single particles containing bacteria may represent a colony consisting of many cells, leading to a further underestimation of their abundance (Tong and Lighthart, 2000).

Despite these limitations, cultivation methods have the advantage that they are far less expensive than molecular techniques and can give an indication of the number of viable cells in the air, for species that respond well to the culturing method used. Cultivation is particularly useful for targeting individual species or groups of microorganisms and for creating culture collections. Culture studies can also characterise certain bacterial strains by various biochemical methods and give qualitative information about relative changes in the concentration over the course of days or season.

3.2.2. Light microscopy.
In addition to cultivation, microscopic techniques have been extremely important to the history and development of PBAP analysis and continue to be invaluable tools. Light microscopy of various types has been applied to the characterisation of collected PBAP (Spurny, 1994; Cox and Wathes, 1995 and references therein). For pollen, it still remains the most common analysis method. Simple optical microscopy was the first technique to be applied to PBAP analysis in the seventeenth century (e.g. Miquel, 1883) and continues to be utilised extensively. But, it has to be taken into consideration that particles <2 μm are only visible as dots under an optical microscope and thus cannot be analysed in detail according to their size and shape. Aerosol samples collected by sedimentation and impaction devices can be directly visualised and counted by light microscopy. If the sampling device used is volumetric, the concentration of particles in the air can be quantified. However, the identification of biological particles via direct counting is both very tedious and somewhat subjective, as the particles must be counted by eye. Various traditional stains can be used in combination with light microscopy, including methylene blue for simple examination, and Gram staining and other differential staining techniques that aid classification into groups of species. Protein staining gives an estimate of all (total) PBAP (Matthias-Maser and Jaenicke, 1995). For the analysis of the diversity and composition of bacteria and fungi, microscopic analyses are not usually reliable, as small non-descript spores and hyphae or fragments of fungal tissues cannot be classified (Pitt and Hocking, 1997). Some fungi or bacteria may remain morphologically

undistinguishable or may only be identifiable to a class or family level.

3.2.3. Fluorescence microscopy.

3.2.3. Fluorescence microscopy. Fluorescence microscopy has been applied both to look at the autofluorescence of PBAP (Pöhlker et al., 2011), and especially with the use of fluorescent dye labelling (Karlsson and Malmberg, 1989; Hernandez et al., 1999). The most common traditional method for determining the total count of environmental microorganism is direct fluorescence microscopy, either by taking advantage of the autofluorescence of certain biological compounds or by using samples that have been treated with a fluorescent dye, most commonly 4.6-diamidino-2-phenylindole (DAPI) or acridine orange (Francisco et al., 1973; Hobbie et al., 1977; Kepner and Pratt, 1994; Matthias-Maser and Jaenicke, 1995; Harrison et al., 2005). Acridine orange binds to both DNA and RNA, fluorescing green when bound to DNA and red when bound to RNA and some mucins. DAPI fluoresces blue when bound to DNA and yellow when unbound or bound to a non-DNA material. Traditionally, particles have been classified and counted by a human investigator, taking into account the size and morphology of stained particles. Epifluorescence microscopy permits counting of the total number of unlysed cells containing DNA; a number that includes both viable and non-viable microorganisms. It is not always possible to unambiguously distinguish different types of biological particles, such as bacterial and fungal spores, via fluorescence microscopy.

However, the colour of autofluorescence combined with the application of fluorescent stains can be used to distinguish some broad groups of microorganisms. Fluorescence microscopy is both tedious and labour intensive, although the use of fluorescence aids the identification of biological particles compared to light microscopy. Recently, more automatic techniques have been attempted, including computer analysis of microscopic images (Carrera et al., 2005) and fluorescence spectroscopy (Reyes et al., 1999; Courvoisier et al., 2008). Other modern fluorescence-based techniques will be described in the next section.

3.3. Modern analysis methods

3.3.1. Molecular techniques

3.3.1.1. Chemical tracers: Chemical tracers, such as the sugar alcohols mannitol and arabitol, can be used to not only assess the abundance of PBAP, especially fungal spores in air particulate matter, but also characterise other aerosol types (Hensel and Petzhold, 1995; Graham et al., 2003; Graham et al., 2004; Lau et al., 2006; Elbert et al.,

2007; Yttri et al., 2007; Bauer et al., 2008a; Engling et al., 2009; IInuma et al., 2009; Burshtein et al., 2011). A number of other chemical tracers have been used as proxies for various types of biological aerosol particles, such as endotoxins, mycotoxins, glucan, ergosterol, extracellular polymeric substances, carbohydrates, proteins, peptides, sugars and adenosine triphospate (ATP). These can be analysed by a wide range of instrumental and bioanalytical techniques such as chromatography coupled to mass spectrometry, spectrophotometry, fluorescence spectroscopy, immunoassays, dye assays, etc. (Griffith and DeCosemo, 1994; Reponen et al., 1995; Franze et al., 2005; Pöschl, 2005; Demirev and Fenselau, 2008).

Chemical tracer analysis has the advantage of providing quantitative information, but it does usually not provide information about the identity and biodiversity of PBAP on the species level.

3.3.1.2. Nucleic acid sampling and extraction: For the study of biological aerosols molecular techniques, e.g. those based on molecular genetic analyses, have some advantages compared to traditional methods. The results can enable the identification and quantification of culturable as well as uncultivable microorganisms, of viable and dead cells, and of plant and animal fragments (Després et al., 2007).

To analyse biological aerosols with molecular genetic tools, biological aerosols need to be collected and the nucleic acids extracted. Biological aerosols are either collected in culturing media (liquid or plates) or water (Boreson et al., 2004), special biological aerosol particle collectors (e.g. the Wetted-wall Cyclone sampler (Biotrace) in Maron et al. (2006)) or on appropriate air filter samples. Several different filter types have already successfully been used for the DNA analysis but not been compared quantitatively to each other (e.g. glass fibre filters (Després et al., 2007; Fröhlich-Nowoisky et al., 2009); quartz fibre filters and polypropylene filtres (Després et al., 2007); cellulose nitrate filtres (Després et al., 2007; Bowers et al., 2010); Celanex polyethylene terephthalate filtres (Brodie et al., 2007); borosilicate filtres (DeSantis et al., 2005) etc.).

The basis for most molecular analyses techniques is the successful extraction of DNA. Every cell carries this molecule: eukaryotes carry DNA in the form of chromosomes within the cell nucleus, whereas prokaryotes and archaea lack a nucleus and carry DNA in genophores directly within their cell body. During the DNA extraction processes, proteins are denatured and separated together with lipids, pigments, cell wall fragments and organelle structures.

DNA extraction protocols vary according to the tissue for which they are used. Plant cells, with strong cell walls, present different extraction challenges than animal tissue cells. Endospores of bacterial and fungal spores have very

strong cell walls that need to be broken down before DNA extraction. Thus, some compromise is always required in selecting a DNA extraction method for ambient air filter samples that contain a mixture of various organisms and tissue types. Either the DNA is extracted using a generic method that does not exclude any tissue type but is also not ideally matched to any specific type such that some organisms and tissue types are undersampled, or the DNA is extracted using a method specific to a particular organism or tissue type, and other types are undersampled. Thus, for ambient samples that include a mixture of many types of biological material, PBAP that contain thick membranes or cell walls could elude extraction of DNA by a generic method, leading to an underestimation of such species. Usually, commercial kits can be used for the extraction (e.g. soil DNA extraction kit (Després et al., 2007; Fröhlich-Nowoisky et al., 2009)); Fast Prep 120 agitator together with Spin column of MolBio Laboratories (DeSantis et al., 2005); alternatively, some investigators develop their own extraction methods (e.g. Boreson et al., 2004; Maron et al., 2005).

3.3.1.3. Amplification of genomic DNA: The DNA extract of an air filter sample still contains the genomic DNA of all sorts of organisms; thus, it is a mixture of DNA from living and dead material of fungi, bacteria, archaea, plants, animals or viruses. To be able to identify single genera or species, it is necessary to enrich the DNA of the organism of interest relative to other genomes. The PCR efficiently amplifies characteristic regions of the DNA of a species, or a group of species, for detailed analyses. The method is based on thermal cycling in which the DNA is heated, thereby separating the double strands. Short DNA sequences, called primers, attach to matching sequences on the single stranded DNA that mark the borders of the region of interest on the genome. In the final step of PCR, the DNA polymerase enzymatically assembles a new matching DNA strand in the target region using single nucleotides. PCR, followed by genetic sequencing of the amplified DNA, can be used to identify organisms, to understand phylogenetic relationships or to study specific genes. Thus, it is an essential technique when studying the identity, diversity and composition of biological aerosols.

Within every genomic DNA, there are areas that are highly conserved between organisms such as housekeeping genes, whereas other areas vary enormously. The primers used in PCR should ideally attach to highly conserved areas, whereas the sequence between the primers should be diverse and thus uniquely present in the targeted organisms or group of organisms. Areas such as ribosomal RNA genes or the ITS-regions with a huge variability are often used in taxonomic identification studies, as they enable to differentiate between genera or even species and thus can

be used as a fingerprint of a species. For bacteria, e.g. often the 16S rRNA genes are amplified (Moffett et al., 2000).

While amplification followed by taxonomic analysis allows the identification of PBAP species within aerosol samples, it gives no information about the quantity of particular species in the air. Quantitative PCR allows the calculation of the number of DNA template molecules in the DNA extract. Thus, when studying, e.g. a single copy gene within a single bacterial species, it is possible to estimate the number of individuals of this particular species that was present in the air filter sample. This could be an especially valuable tool for studying pathogenic biological aerosol particles.

Although molecular techniques are thought to detect biological aerosols unambiguously, they may not amplify all airborne bacteria in a sample (Peccia and Hernandez, 2006; Fierer et al., 2008). Theoretically, the DNA polymerase can amplify a single DNA copy and thus detect even organisms that are present in minor quantities. But, the sensitivity of the PCR depends on several factors. One major issue is the choice of the primer pair used for the amplification process. Different primer pairs have different specificity and sensitivity (Alvarez et al., 1995; Polz and Cavanaugh, 1998). Thus, while one primer pair might start the amplification from just a single DNA strand, a less sensitive primer pair might need 100 molecules to get started. It is also possible that a primer pair is more sensitive to some species than to others within a targeted group. Although a primer pair might have been designed to perfectly match the target organism, it might also co-amplify other organisms. This is especially important for biological aerosol DNA extracts where many competing DNA molecules may be present, possibly even in higher concentrations than the organism of interest. Literature research can help to find suitable specific primers, but often the specificity of primers is overstated in the literature (e.g. Fröhlich-Nowoisky et al., 2009).

Another important point that must be considered is the possible presence of PCR inhibitors. Substances such as humic acids inhibit the DNA amplification process either by hindering the attachment of polymerase to the primers to initiate amplification, or by binding to the DNA and thereby preventing primers or enzymes from attaching. Different PCR primers as well as DNA polymerases vary in their ability to overcome inhibitory factors. In addition, filter materials on which biological aerosol particles are collected can inhibit PCR (Després et al., 2007).

Finally, although DNA is a stable molecule, which under cool, dark and dry conditions can sometimes be preserved for several thousand years (Pääbo et al., 2004), DNA starts to degrade, breaks into smaller pieces and is chemically modified as soon as an organism dies (Pääbo, 1989; Lindahl, 1993; Höss et al., 1996; Smith et al., 2001). UV

light, ozone and melting-freezing processes speed up these degradation processes, and thus a long residence time of biological material in air leads to deterioration of DNA and loss of genetic information. Pollen grains, as well as many spores of fungi and bacteria, are encased by thick cell walls to protect their DNA from DNA-destroying environmental processes.

3.3.1.4. Restriction fragment length polymorphism techniques: A standard molecular genetic technique is the fragmentation of DNA by a restriction enzyme that cuts the DNA wherever a specific target sequence occurs. The resulting restriction fragments are separated according to their lengths by gel electrophoresis. It can be applied following colony PCR (confirmation of plasmid insertion) to select as many different clones as possible for the sequencing reaction (Fröhlich-Nowoisky et al., 2009). For a broad characterisation of the community structure and diversity of a PBAP sample, the terminal restriction fragment length polymorphism (T-RFLP) technique can be used to get a rough estimate of the diversity and relative abundances (Després et al., 2007; Georgakopoulos et al., 2009). The first step of a T-RFLP is a PCR amplification in which one primer is fluorescently labelled. The PCR products are then digested with a restriction enzyme that cuts each DNA strand at the target sequence, resulting in shorter, labelled fragments. Because the position of the target sequence on the genome varies among bacterial strains, the length of the labelled fragments also varies. The fluorescently labelled end fragments are separated by electrophoresis, and the strand lengths and fluorescence intensities are calculated. The fluorescence intensity of strands of a given length indicates the frequency of the corresponding bacterial strains in the original sample. The genetic diversity indicated by a T-RFLP profile (as measured by the number of different strand lengths) is highly dependent on the choice of the restriction enzyme and the part of the gene used to generate the terminal fragments. If the PCR products are simultaneously cloned and sequenced, the size of the terminal fragment that each will produce can be calculated, and so each sequence can be attributed to a T-RFLP peak (Després et al., 2007; Georgakopoulos et al., 2009).

3.3.1.5. Sequencing methods: To determine the identity of the genomes obtained from atmospheric aerosol samples, the PCR products are often cloned and sequenced (e.g. Boreson et al., 2004; Maron et al., 2005; Després et al., 2007; Fierer et al., 2008; Bowers et al., 2009; Fröhlich-Nowoisky et al., 2009; Georgakopoulos et al., 2009). Species can often be identified by comparing the obtained sequences with those that are already available in online databases, e.g. that of the National Center for Biotechno-

logy Information (NCBI). The BLAST search[4] is the easiest way to search for matching sequences. If a new organism (e.g. new bacterial strain) is found, it is possible to identify the most closely matching sequences already available in the database. For bacteria, the generally accepted levels of discrimination are 97–99% similarity for species and 95–97% for genera; for fungi, clustering sequences with 97% or greater sequence similarity are accepted (O'Brien et al., 2005; Bowers et al., 2009; Fröhlich-Nowoisky et al., 2009; Georgakopoulos et al., 2009). The traditional sequencing technique is using a chain termination (Sanger and Coulson, 1975; Sanger, 1981). The sequencing process is essentially another PCR but only one primer instead of two is used. The reaction mix contains not only the standard DNA bases (deoxynucleotide-triphosphate, dNTP) but also chain terminator dideoxynucleotide-triphosphates (ddNTPs) that are labelled with fluorescent dyes that emit light at different wavelengths (dye-terminator sequencing). The incorporation of a ddNTP results in a chain termination, and the fluorescence peaks are detected after capillary electrophoresis resulting in the DNA sequence.

The high demand for low-cost sequencing in recent years has led to the development of high-throughput sequencing technologies. In these technologies, the sequencing process is parallelised for several samples, and thus in a short time thousands or millions of sequences are produced. One high-throughput technique, 454 pyrosequencing, has been applied successfully several times in biological aerosol research (Bowers et al., 2009, 2011). The DNA is amplified within an oil droplet by the so-called emulsion PCR. Each oil droplet contains a single DNA template attached to a single primer-coated bead that then forms a clonal colony. The sequencing machine contains many picolitre-volume reactions areas, each containing a single bead and sequencing enzyme. Pyrosequencing uses luciferase to generate light for detection of the individual nucleotides added to the nascent DNA, and the combined data are used to generate sequence readouts. For studies in which the taxonomic identification of biological aerosols is anticipated, the amplified sequences must have a minimum length to enable differentiation at the genus or species level. Often, this minimum length is around 600–1000 bp (base pairs). In traditional sequencing, this length can be reached easily, whereas in high throughput sequencing the length of the different sequences is usually only around 300–400 bp. Thus, with current high-throughput techniques, it is often not possible to identify biological aerosol particles on a species or genus level.

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[4]Provided by NCBI http://blast.ncbi.nlm.nih.gov/Blast.cgi, 28 March 2011.

3.3.1.6. Hybrid and chip technology: Microarrays can be used for the characterization of PBAP (Wilson et al., 2002; Brodie et al., 2007; Georgakopoulos et al., 2009). Species or group specific probes (e.g. bacterial 16S rRNA genes of DNA; Loy and Bodrossy, 2006) are fixed on glass slides. DNA from atmospheric samples is fluorescently labelled and can hybridise with the DNA on the microarray if complementary sequences exist in the microarray. The sequence is determined from the position of the fluorescence on the chip. This technology was recently used on atmospheric aerosol samples for bacterial 16S rRNA genes (Wilson et al., 2002; Brodie et al., 2007). Both studies compared the cloning and sequencing method with microarray technology that was found to be more sensitive in detecting bacterial taxa.

3.3.2. Optical methods. Most of the above-mentioned methods for detecting PBAP are limited to offline analyses that can be time consuming, costly and which often provide measurements that suffer from poor time resolution (hours/days). However, much effort has been invested in the last decades, largely by military research facilities interested in quick detection of bio-warfare agents, to be able to detect biological aerosols in real time and with high time resolution. However, a comprehensive review of all modern methods for PBAP detection is well beyond the scope of this text and the following section is intended to present an overview of the most important classes of techniques. It focuses on field-based techniques, although some techniques that are primarily laboratory based are also discussed, as they may have important relevance to ambient detection.

3.3.2.1. On-line autofluorescence methods: All biological materials contain fluorophores that may be helpful for identification. Among most existing instruments that utilise biological auto-fluorescence for online determination of biological aerosol particle concentration, the choices of wavelength for the excitation source can generally be classified into one of two regions. Sources that provide light in the region of approximately 350–370 nm enable detection of reduced pyridine nucleotides (e.g. NAD(P)H) and riboflavin that are biological molecules linked to cellular metabolism (Harrison and Chance, 1970; Eng et al., 1989; Kell et al., 1991; Li et al., 1991; Iwami et al., 2001). Detection of auto-fluorescence under these conditions may indicate the presence of viable biological material in the aerosol particles, although other biological molecules (e.g. chlorophyll, cellulose) can also auto-fluoresce under many environmental conditions. The second region of fluorescence excitation commonly utilised by biological aerosol instrumentation is approximately 260–280 nm and highlights amino acids, such as tryptophan, tyrosine and

phenylalanine that are present in all proteins (e.g. Teale and Weber, 1957; Pöhlker et al., 2011).

Thus, it can be broadly stated that detection of fluorescence by this class of instruments allows determination of fluorescent biological aerosol particles (FBAP). However, different instrument designs measure and report different fractions of the PBAP and comparisons across instruments should be conducted with this in mind. Among the uncertainties involved is the possibility that material of non-biological origin will also fluoresce within a given particle, causing a positive artifact. However, non-biological particles producing such artefacts are unlikely to contribute significantly to the coarse (>1 μm) fraction of ambient particulate mass (Huffman et al., 2010) and may also exhibit much weaker fluorescence than biological particles. For example, results of a study performed in remote Amazonia indicated that coarse FBAP closely approximated PBAP concentrations and size distributions (Pöschl et al., 2010). It is also known that not all biological microorganisms or fractions will fluoresce under the experimental conditions of such instruments, and opaque or absorbing PBAP are likely to fluoresce only very weak at best (Pöhlker et al., 2011). The weak fluorescence of some PBAP suggests that fluorescence measurements underestimate the total biological material present. Further investigation will be required to achieve full understanding of the response of fluorescence-based biological aerosol particle detectors to all types of biogenic aerosol particles, and to quantify potential interferences by fluorescence of non-biological particles. However, our present understanding is that FBAP can generally be regarded as an approximate lower limit for the actual abundance of PBAP (Huffman et al., 2010).

The Ultraviolet Aerodynamic Particle Sizer[5] (UV-APS) was the first commercially available, fluorescence-based instrument for real-time analysis of biological aerosols (Hairston et al., 1997; Brosseau et al., 2000). The UV-APS measures the aerodynamic diameter and side scatter parameter (analogous to the optical diameter) of incoming particles by measuring their time-of-flight between two lasers (633 nm) and then detects fluorescence in the wavelength range of 420–575 nm after excitation by a pulsed ultraviolet laser (Nd:YAG, 355 nm). An example of UV-APS measurement data is given in Fig. 4. This shows time series and size distributions of FBAPs detected with a UV-APS at a site in central Europe (Mainz, Germany, October 2006). The figure highlights the ability of the UV-APS to measure FBAP size distributions of discrete particle events with much higher time and size resolution than is

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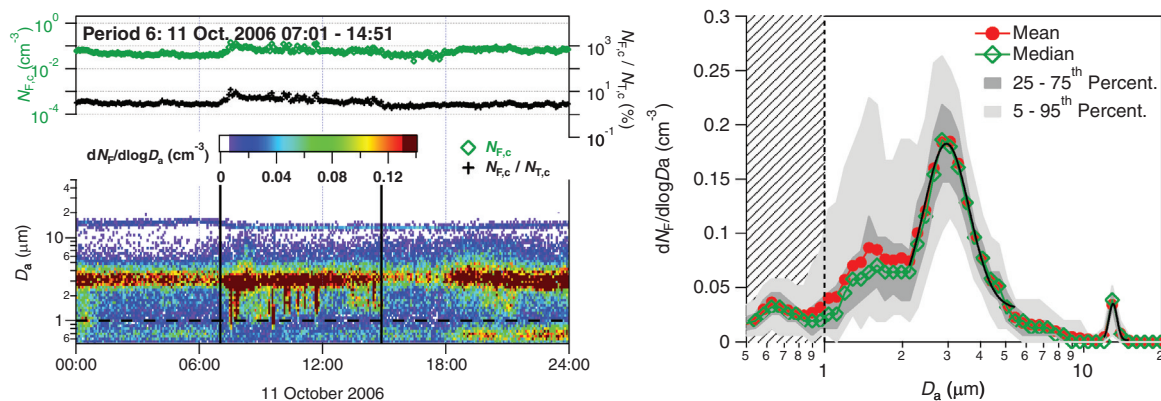[5]UV-APS; TSI Inc., Model 3314, St. Paul, MN

Fig. 4. Characteristic time series and number size distribution of fluorescent biological aerosol particles (FBAPs) measured with an ultra-violet aerodynamic particle sizer (UV-APS) in central Europe (Mainz, Germany, October 2006). The peaks at ~ 1.5, ~ 3 and ~ 13 µm can be attributed to bacteria, fungal spores, and pollen. $N_{F,c}$ is the number concentration of FBAPs, and $N_{T,c}$ is the number concentration of total aerosol particles with aerodynamic diameters $D_a > 1$ µm; $dN_F/dlogD_a$ is the number size distribution function of FBAPs (Huffman et al., 2010).

achievable by most traditional sampling and detection methods (Huffman et al., 2010).

The Wide Issue Bioaerosol Spectrometer (WIBS) is also available in limited commercial production and not only provides conceptually similar information to the UV-APS but also provides a rough estimate of particle sphericity (Kaye et al., 2000, 2005). Incoming particles are first optically sized by measurement of scattered laser light. UV pulses at ~ 280 and ~ 370 nm from a xenon flash lamp excite each particle, and multiple bands of fluorescent emission in the range of 310–400 nm (for 280 nm excitation) and 420–650 nm (for 280 and 370 nm excitation) are recorded.

A number of other instruments have been developed for military research use and have not been commercialised or widely used for measurements published within peer-reviewed literature. However, these technical and scientific developments have been significant contributions to the scientific community (e.g. Hill et al., 1995; Cheng et al., 1999; Reyes et al., 1999; Seaver et al., 1999; Kopczynski et al., 2005; Cabredo et al., 2007; Campbell et al., 2007; Manninen et al., 2008; Pan et al., 2009; Sivaprakasam et al., 2009).

Although the development of such instruments has left a detailed trail in publically accessible military reports and peer-reviewed literature, ambient measurements by such techniques have been less frequently documented or de-classified. An early generation UV-APS (Ho, 2002) was used for short periods to measure background FBAP concentrations at several military locations within Canada and Sweden (Ho and Spence, 1998; Ho et al., 2004), and a different LIF spectrometer design was utilised for detection of FBAP in ambient air in several US locations (Pinnick

et al., 2004; Pan et al., 2007; Pan et al., 2009). Recently, fluorescence measurements of biological aerosols have also been reported in more detail for tropical rainforest air (Prenni et al., 2009; Gabey et al., 2010; Pöschl et al., 2010) as well as in two urban European locations (Huffman et al., 2010; Gabey et al., 2011).

3.3.2.2. Flow cytometry: Flow cytometry has also long been an important tool in the investigation of ambient PBAP. Among the papers that report successful applications of flow cytometry to real-time investigation of biological aerosol are those by Sincock et al. (1999), Chen and Li (2005) and Chen and Li (2007). Fluorescent in situ hybridization (FISH) flow cytometry has been used by a number of groups to characterise airborne bacteria and aerosolised byproducts (e.g. Lange et al., 1997). Using a flow, cytometric system (Ho and Fisher, 1993) investigated *Bacillus subtilis* bacterial spores, and Prigione et al. (2004) developed a flow cytometer that could be selectively applied to the investigation of airborne fungi.

3.3.2.3. LIght Detection And Ranging (LIDAR) and remote sensing: The LIght Detection And Ranging (LIDAR) technique has been utilised to quickly and remotely monitor the presence of PBAP over a larger spatial range. A LIDAR system (Evans et al., 1994) was operated to determine its sensitivity to aerosolised *Bacillus subtilis* spores, and subsequent efforts have investigated LIDAR performance for PBAP detection in more detail (e.g. Simard et al., 2004; Glennon et al., 2009). The detection of fluorescent ambient aerosol was reported for the first time using a LIDAR system (Immler et al., 2005), attributing the signals to a combination of PAH-containing

particles and/or PBAP. Furthermore, it was shown (Sassen, 2008) that pollen can generate strong laser depolarisation in LIDAR backscatter during Alaskan springtime measurements and suggested that pollen plumes may be mistaken for upper cirrus clouds and therefore introduce important errors into identifying aerosols in the atmosphere. Atmospheric optical phenomena caused by pollen also have been reported,[6] and will be discussed briefly in Section 5.

3.3.2.4. Fluorescent and Raman spectroscopy: Fluorescent properties of collected biological aerosols have been widely used for assessment of concentrations and properties of ambient PBAP. Fisar et al. (1990) showed that fluorescence detected from dyed biological aerosol particles could be effectively scaled to more traditionally measured CFUs. Raman spectroscopy has been used for investigation and characterisation of individual pollen grains in a number of different manners by various groups (Laucks et al., 2000; Boyain-Goitia et al., 2003; Kano and Hamaguchi, 2006; Schulte et al., 2008). A particularly interesting technique utilised fluorescence measured from particles impacted on a surface as a pre-selector, before Raman spectroscopy enabled bacterial identification in more detail (Rosch et al., 2006). Surface-enhanced Raman spectroscopy has also been employed to sensitively detect and characterise pollen and bacteria after injection into a silver suspension (Sengupta et al., 2005, 2006, 2007). Raman microscopy has been utilised by Ivleva et al. (2005) for the chemical investigation and discrimination of ambient PBAP. They used a combination of Raman microscopy with multivariate analyses to characterise sampled pollen with the goal of differentiating between allergenic species.

3.3.2.5. Additional optical methods: While the classes of optical techniques mentioned have been most commonly utilised for biological aerosol analysis, a review of the literature highlights the virtually endless list of techniques that have been and could be applied. Among notable additional efforts include the use of X-ray fluorescence (Pepponi et al., 2004) and total internal reflection fluorescence microscopy (TIRFM) (Axelrod, 2008) for the investigation of biological aerosol properties. Infrared vibrational spectroscopy has also been widely used for pollen identification (Pappas et al., 2003; Gottardini et al., 2007; Dell'Anna et al., 2009; Zimmermann, 2010). Scanning electron microscopy (SEM) has been particularly useful at the investigation of PBAP, allowing a close look at the morphology and surface of particles (Karlsson and Malmberg, 1989; Wittmaack et al., 2005; Coz et al., 2010; Pöschl et al., 2010; Gilardoni et al., 2011).

A recent study has applied Scanning Transmission X-ray Microscopy with Near-Edge X-ray Absorption Fine Structure (STXM-NEXAFS) spectroscopy to the study of PBAP (Pöhlker, personal communication). This technique allows the structural examination of particles with a resolution down to about 30 nm, combined with spatially resolved chemical characterisation. It is suitable for the determination of the major elements, carbon, nitrogen and oxygen, as well as some minor elements, e.g. iron and chlorine. In addition to the measurement of elemental abundances, it can also yield information on the bonding state of the various elements. Using STXM-NEXAFS, Pöhlker (personal communication) could show that the coarse fraction of the Amazonian aerosol consisted predominantly of intact PBAP.

3.3.3. Non-optical methods. Several reviews of modern techniques of biological aerosol detection and analysis have been published (Spurny, 1994; Ho, 2002; Douwes et al., 2003; Lim et al., 2005; Kuske, 2006) and so, again, only highlights of important classes of non-optical modern techniques will be discussed here.

3.3.3.1. Mass spectrometry: Advances in mass spectrometry (MS) have been utilised in many areas of physical and biological science in the last decades to provide detailed information about chemical composition. The analysis of biological aerosols has been no different, and many different MS techniques have been employed for PBAP characterisation. Matrix-Assisted Laser Desorption Ionization Time-Of-Flight (MALDI-TOF) has been successfully applied in several PBAP studies (Kim et al., 2005; van Wuijckhuijse et al., 2005; Kleefsman et al., 2008; Russell, 2009). Parker et al. (2000) developed an instrument that utilised ion-trap mass spectrometry for detection and analysis of pollen, bacteria and other aerosol types. Stowers et al. (2006) demonstrated the utility of laser-induced fluorescence as a pre-selector before more detailed MS identification. Lawrence Berkeley National Lab has also utilised a similar concept for its biological aerosol mass spectrometry (BAMS) instrument (e.g. Fergenson et al., 2004) and has deployed the instrument in a number of field locations. Other real-time MS instruments designed primarily for other aerosol-related detection purposes have also been applied to PBAP characterisation. For example, an Aerodyne Aerosol Mass Spectrometer (AMS) was deployed in Amazonia, Brazil and was able to detect molecular ion markers in submicron aerosol consistent with the presence of biological aerosols (Chen et al., 2009; Pöschl et al., 2010; Schneider et al., 2011). Pratt et al. (2009) utilised an Aerosol Time-of-Flight Mass Spectrometer (ATOFMS) to detect the presence of biological aerosols as ice nuclei

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during some flights of an aircraft campaign in the Western United States. While not technically a mass spectrometer, both Dworszanski (1997) and Snyder et al. (2001) report development of automated instruments that utilise pyrolysis-gas chromatography in front of an ion mobility spectrometer for rapid detection of biological aerosol particles in the field.

3.3.3.2. Breakdown spectroscopy: Many groups have also utilised different types of breakdown spectroscopy (BS) to identify elemental composition as means of biological aerosol detection and analysis, although these have not been as widely applied to ambient measurements. Laser-induced breakdown spectroscopy (LIBS) has easily been the most common form of BS method and has been employed to characterise pollen (Boyain-Goitia et al., 2003), and fungal spores (Hybl et al., 2003), bacteria (Morel et al., 2003) and a variety of biological aerosol particle types (Samuels et al., 2003). Other forms of elemental analysis such as spark-induced breakdown spectroscopy (SIBS), particle-induced X-ray emission (PIXE) and various forms of combustion analysis have also been utilised for laboratory study of biological aerosol (Sarantaridis and Caruana, 2010; Schmidt and Bauer, 2010).

3.3.3.3. Miscellaneous non-optical-methods: As has been the case for recently developed optical methods of biological aerosol analysis, a large variety of non-optical techniques of chemical and physical analysis have been employed. Bioluminescence and chemiluminescence have been extensively explored for potential analytical benefits, and much of this effort has focused on the detection of ATP within collected aerosol (e.g. Lee et al., 2008; Seshadri et al., 2009; Yoon et al., 2010). Electrochemical, immunochemical and immune biological methods have also been investigated for ambient PBAP characterisation (Rishpon et al., 1992; Spurny, 1994; Sarantaridis and Caruana, 2010; Schmidt and Bauer, 2010). It should be noted here that complementary instruments such as biological aerosol particle concentrators have also helped enable analyses by a variety of instruments (e.g. Pan et al., 2004).

4. Atmospheric relevance

4.1. Atmospheric transport of biological particles

Particles in the atmosphere, both biological and non-biological, are transported primarily together with air currents, as well as vertically downwards by gravitational sedimentation and inside of airborne water droplets and ice crystals. Particles are removed from the air either by sedimentation and deposition onto the ground and plant or other surfaces, or through washout by precipitation.

Depending on their size and aerodynamic properties, the average residence time of various biological particles in the atmosphere can range from less than a day to a few weeks. We do not attempt a complete review of atmospheric transport processes and their particular impact on biological aerosols here, but only give a brief overview of some key research areas. Existing reviews cover aspects of this topic in more detail (Gregory, 1973; Niklas, 1985; Aylor, 1986; Nagarajan and Singh, 1990; Brown and Hovmøller, 2002).

Dry deposition (sedimentation and interception/impaction onto surfaces) is the most important removal mechanism for particles tens of microns in diameter or larger. Dry deposition rates are characterised primarily by the particle's aerodynamic diameter (diameter of a spherical particle of unit density with the same terminal velocity in air as the particle in question (e.g. Hinds, 1999)). Because biological particles often have complex structure (rough surfaces, internal pores and asymmetric shape), their physical and aerodynamic sizes can differ significantly. In particular, certain fungal spores, pollen and seeds are adapted to be aerodynamically buoyant, to promote long-range airborne transport. Observations show that the aerodynamic diameter may be either larger or smaller than the physical diameter, with considerable variation between species (Gregory, 1973; Fig. 3, p. 17; Madelin and Johnson, 1992; Reponen et al., 1998; Reponen et al., 2001), and microorganisms may sometimes be present in the atmosphere in clumps or attached to other particles (Lacey, 1991; Tong and Lighthart, 2000).

For particles ~ 0.1–10 μm in diameter, washout by falling precipitation is the most efficient removal mechanism. A single rain event (even a slight drizzle) can efficiently remove a large percentage of particles from the air in many circumstances (McDonald, 1962).

In spite of limited differences related to buoyancy and IN activity, biological particles can be expected, to a good first approximation, to be transported in the atmosphere similarly to mineral dust and are treated similarly to dust in most model studies of atmospheric dispersion. Desert dust particles of a similar size to bacteria-carrying particles are well known to be transported over long distances, particularly during intermittent dust storms that are visible to satellites. Biological particles, undistinguishable to satellites, can be transported over long distance in a similar fashion, as is borne out by case studies showing marked changes in the concentration and composition of airborne microorganisms during some dust transport events (e.g. Bovallius et al., 1978; Prospero et al., 2005; Jeon et al., 2011); global atmospheric model simulations produce similar results (Burrows et al., 2009b; Wilkinson et al., 2012).

A wide variety of approaches have been used for modelling the transport of biological particles on different spatial scales: Gaussian plume models (distances up to

∼100 m; Ganio et al., 1995; Skelsey et al., 2008), Lagrangian stochastic models (Jarosz et al., 2004), regional-scale models (Helbig et al., 2004; Sofiev et al., 2006) and global climate and transport models (Burrows et al., 2009b; Wilkinson et al., 2012). Most studies of the airborne dispersal of biological particles have focused on the spread of specific human, animal and plant diseases on the local or regional scale (Donaldson et al., 1982; Gloster et al., 1982; Aylor et al., 2003; Isard et al., 2005). Others have addressed the potential for dispersal and cross-fertilization of GM organisms (Aylor et al., 2003; Jarosz et al. 2004) and seed dispersal (Nathan et al., 2002).

4.2. PBAP as cloud condensation nuclei

Aerosol particles form the nucleus for the condensation of cloud droplets, and their number and properties influence cloud microphysical properties. How active particles are as cloud condensation nuclei (CCN) depends on their size and hygroscopicity (Petters and Kreidenweis, 2007). Primary biological aerosol particles are generally assumed to be efficient CCN, provided that their surfaces are wettable (Andreae and Rosenfeld, 2008; Ariya et al., 2009). It has been suggested that the largest PBAP (e.g. pollens grains) may act as the so-called 'giant CCN', i.e. they may form cloud droplets at lower supersaturations than most other aerosol particles and quickly grow to large droplet sizes, thereby facilitating rain formation (Dingle, 1966; Möhler et al., 2007; Pope, 2010).

Table 5 lists measurements of hygroscopic growth of bacteria, fungal spores, pollen and algal exudate below water saturation and shows critical supersaturations that have been determined for some bacterial species and algal exudate (exopolymer secretions, EPS). Below the saturation point of water, hygroscopicity is quantified by the diameter increase relative to the dry diameter ('diameter growth factor') or by the mass of the water taken up at a certain relative humidity (RH) compared to the dry mass. The diameter growth factors (GF) observed for bacteria and fungal spores are usually modest (GF ∼1.05 to 1.3 at RH = 98%) compared to those of inorganic salt particles such as sodium chloride (GF ∼1.65 at RH = 98%) (Lee et al., 2002). Pollen grains usually show no or only little increase in geometric size at increasing relative humidities, but can take up substantial amounts of water, e.g. up to three times their dry weight at RH = 95% (Diehl et al., 2001). Critical supersaturations for bacteria have been reported over a wide range between 0.07 and more than 2% (Franc and DeMott, 1998; Bauer et al., 2003). Algal exudate, which is mixed into sea spray particles, reduces the hygroscopicity and CCN activity relative to artificial seawater devoid of exudate (Wex et al., 2010; Fuentes et al., 2011).

4.3. PBAP as ice nuclei

Cloud water droplets do not freeze directly at 0°C but can remain in a supercooled liquid state down to temperatures of approximately −38°C. At higher temperatures, aerosol particles are required as ice nuclei to initiate ice formation via heterogeneous freezing, i.e. the formation of ice germs by the aid of crystal-like structure elements or other the so-called active sites on the particle surface. If an ice nucleus (IN) is contained inside a liquid droplet when initiating freezing, the process is termed 'immersion freezing'. 'Condensation freezing' is a special case of immersion freezing, in which the CCN of a cloud droplet acts as an IN during the condensational growth phase. If a supercooled droplet collides with an aerosol particle and freezes as a result of the collision, one speaks of 'contact nucleation'. On dry particles ('deposition nucleation'), ice can also form directly from the vapour phase (Pruppacher and Klett, 1997). Freezing of a relatively small number of cloud droplets can trigger glaciation, i.e. turning a whole cloud or a region within a cloud into pure ice. Glaciation is driven by the different values of the saturation vapour pressure over supercooled liquid water and over ice, which leads to depositional growth of the ice crystals at the expense of evaporating droplets once the relative humidity falls below water saturation (Wegener-Bergeron-Findeisen process, Findeisen, 1938). This process is connected to the formation of large crystals that tend to fall out as precipitation. Furthermore, ice-multiplication processes can occur, in which additional ice crystals are produced from existing ice crystals, for example due to the formation of ice splinters during riming of ice particles (Hallett and Mossop, 1974).

In numerous studies, it has been established that mineral dust particles are relatively efficient ice nuclei. At lower temperatures, soot particles also can nucleate ice. Interestingly, the most active IN (those nucleating ice at the highest subzero temperatures) discovered so far are of biological origin. Overviews of biological ice nucleation measurements and discussions of their possible implications are given in previous reviews (Lee et al., 1995; Szyrmer and Zawadzki, 1997; Möhler et al., 2007; Delort et al., 2010; DeMott and Prenni, 2010). Here, we summarise the observational basis of biological ice nucleation seen in laboratory experiments and, as far as available, in the atmosphere, including both, historical and recent measurements. With the help of modelling studies, the observations are put into the context of typical atmospheric concentrations and atmospherically relevant processes.

4.3.1. Laboratory studies of ice nucleation active biological particles. Since the first ice-nucleating biological particles were discovered, numerous microorganisms have

Table 5. Compilation of laboratory measurements of the hygroscopic properties of biological particles (n.a. = data not available)

Species	Diameter, D_{ve}–volume equivalent, D_{gma} geometric mass aerodynamic, D_{mma} – mass median aerodynamic, D_a – aerodynamic	Measurements at subsaturation		Measurements at supersaturation		References
		Maximum growth factor at RH	RH at which hygroscopic growth was measured	Critical supersaturation	CCN/CN ratio	
Bacteria						
Pseudomonas syringae, Erwinia herbicola	n.a.	–	–	activation observed at 0.5%	n.a.	Snider et al. (1985)
Erwinia carotovora	3 μm (maximum cellular dimension)	–	–	0.2% to 2.2%	≤ 0.5	Franc and DeMott (1998)
Arthrobacter agilis	1.1 μm D_{ve}	–	–	0.11%	1.03 ± 0.7	Bauer et al. (2003)
"new species"	1.1 μm D_{ve}	–	–	0.11%	0.88 ± 0.5	Bauer et al. (2003)
Sphingomonas echinoides	1.2 μm D_{ve}	–	–	0.09%	0.92 ± 0.6	Bauer et al. (2003)
Sphingomonas echinoides – fixed	1.2 μm D_{ve}	–	–	0.07%	0.99 ± 0.4	Bauer et al. (2003)
Saccharomonospora viridis	1.15 μm D_{gma}	1.3 at 95%	95%	–	–	Madelin and Johnson (1992)
Streptomyces albus	1.15 μm D_{gma}	1.09 at 95%	95%	–	–	Madelin and Johnson (1992)
Bacillus subtilis	0.94 μm D_{mma}	~1.22 at 90%	10–90%	–	–	Johnson et al. (1999)
Pseudomonas syringae	0.89 μm D_{mma}	~1.15 at 90%	10–90%	–	–	Johnson et al. (1999)
Escherichia coli	0.63 μm D_a	1.34 at 98%	20–98%	–	–	Lee et al. (2002)
Bacillus subtilis	0.75 μm D_a	1.16 at 98%	20–98%	–	–	Lee et al. (2002)
Fungal spores						
Aspergillus flavus	3.3 μm D_{gma}	1.15 at 95%	95%	–	–	Madelin and Johnson (1992)
Aspergillus fumigatus	1.9 μm D_{gma}	1.16 at 98%	95 and 98%	–	–	Madelin and Johnson (1992)
Cladosporium cladosporioides	2.3 μm D_{gma}	1.12 at 98%	95 and 98%	–	–	Madelin and Johnson (1992)
Paecilomyces variotii	2.5 μm D_{gma}	1.06 at 98%	95 and 98%	–	–	Madelin and Johnson (1992)
Penicillium chrysogenum	2.6 μm D_{gma}	1.07 at 98%	95 and 98%	–	–	Madelin and Johnson (1992)
Penicillium minioluteum	1.6 μm D_{gma}	1.12 at 98%	95 and 98%	–	–	Madelin and Johnson (1992)
Scopulariopsis brevicaulis	5.1 μm D_{gma}	1.08 at 95%	95%	–	–	Madelin and Johnson (1992)
Penicillium brevicompactum	2.9 μm D_{gma}	~1.05 at 90%	30–100%	–	–	Reponen et al. (1996)
Penicillium melinii	2.4 μm D_{gma}	~1.08 at 90%	30–100%	–	–	Reponen et al. (1996)
Aspergillus versicolor	2.1 μm D_{gma}	~1.07 at 90%	30–100%	–	–	Reponen et al. (1996)
Aspergillus fumigatus	2.1 μm D_{gma}	~1.06 at 90%	30–100%	–	–	Reponen et al. (1996)
Cladosporium cladosporioides	1.8 μm D_{gma}	~1.04 at 90%	30–100%	–	–	Reponen et al. (1996)

Table 5 (*Continued*)

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Species	Diameter, D_{ve}–volume equivalent, D_{gma} geometric mass aerodynamic, D_{mma} – mass median aerodynamic, D_a – aerodynamic	Measurements at subsaturation		Measurements at supersaturation		References
		Maximum growth factor at RH	RH at which hygroscopic growth was measured	Critical supersaturation	CCN/CN ratio	
Pollen						
various ragweed, amaranth-chenopod and grass pollens	n.a.	Mass increase by up to a factor of 2	'very dry' to 'moist'	–	–	Durham (1943)
Ambrosia artemisiifolia	20 μm	Effective density increase: 1.52 at 93–100%, no geometric growth	11–100%	–	–	Harrington and Metzger (1963)
various pollens (deciduous trees, conifers and grasses)	22 to 115 μm	Mass increase by up to a factor of 4 at 95%	73 and 95%	–	–	Diehl et al. (2001)
Daffodil, water birch and pussy willow pollens	25 μm (birch pollens)	Mass increase by up to a factor of 1.3 at 85%	2– ∼85%	≤0.002% (calculated)	–	Pope (2010)
Algal exudates (extracellular polymeric substances, EPS)						
Artificial seawater with diatomaceaous and nanoplancton exudates	40–105 nm	∼2.5 at 92%, lower than for artificial seawater devoid of exudates	45–92%	0.1 to 0.5% for sizes between 40 and 105 nm	–	Fuentes et al. (2011)
Artificial seawater with exudate of four different algal species	25–500 nm	∼4 at 99%, lower than for artificial seawater devoid of exudates	75–99%	0.1 to 0.4% for diameters between 40 and 100 nm	–	Wex et al. (2010)

been screened for ice nucleation activity. A selection of results is summarised in Table 6. Listed are the highest temperatures at which ice nucleation was observed, which are often cited as key findings of the experiments. Equally important is the fraction of ice-nucleating particles to total particles because often the apparent freezing onset depends on the particle concentration (Yankofsky et al., 1981). For many biological species, only a small fraction of the total particles (i.e. in the case of bacteria: cells) actually nucleates ice, even at relatively low temperatures. Nevertheless, the entire species or strain is referred to as 'ice nucleation active' (INA). The IN number fractions at different temperatures, as far as they are available from the experiments in Table 6, are displayed in Fig. 5.

Many studies listed in Table 6 used biological particles sampled not from the atmosphere, but from plants, lichens, soils, ocean water and insect guts. Some of them were cultivated under favourable conditions being tested for IN activity. It can thus be questioned whether the investigated samples are representative of biological aerosols. Most studies employ the so-called droplet freezing assay with rather large volumes (several μl) of particle suspensions (thus testing for immersion freezing). Only a few experiments employ atmospherically relevant droplet sizes (e.g. Möhler et al., 2008) or test for other nucleation modes (e.g. Levin and Yankofsky, 1983).

Among bacterial ice nucleators, *Pseudomonas syringae* is the most common. Other INA species include *Pseudomonas fluorescens* and *Erwinia herbicola*. In general, not all strains within a species are INA, and also within the INA strains, the fraction of ice-nucleating cells varies significantly (Hirano and Upper, 1995). Active number fractions between 10^{-8} and close to 1 are reported, and the onset of ice nucleation can be seen at temperatures between -2 and $-10°C$ (Table 6 and Fig. 5). Species with intermediate IN activity begin ice nucleation only at lower temperatures (e.g. Mortazavi et al., 2008).

A number of fungi (both free living and lichen fungi) were found to nucleate ice at temperatures comparable to INA bacteria (Table 6), some even at $-1°C$. Fungal spores, which are more likely to become airborne than other parts of the fungal thallus, have been observed to nucleate ice at lower temperatures (-10 to $-28.5°C$, Jayaweera and Flanagan, 1982; Iannone et al., 2011). Lichen photobionts (algae or cyanobacteria) are in general less efficient IN than the corresponding lichen fungi (Kieft and Ahmadjian, 1989).

Pollen of various plant species have been shown by a number of studies (Diehl et al., 2001, 2002; von Blohn et al., 2005) to nucleate ice starting at temperatures around $-10°C$ (Table 6). Very high active fractions (up to 1.0) can be reached at $-18°C$ (Diehl et al., 2001). Other biological materials, such as algae, leaf litter and plankton initiate

freezing at temperatures comparable to bacteria and fungi. IN numbers are usually given in relation to the mass of the bulk material, which is of only limited relevance for atmospheric applications, where particle surface area and number fractions matter.

Also shown in Fig. 5 are ice nucleating number fractions for mineral dust particles of atmospherically relevant sizes (median diameters of 0.2–1 μm) in the immersion freezing mode (Niemand, personal communication). The observed ice nucleating fractions for dust range from about 10^{-4} to 10^{-2} at temperatures between -15 and $-28°C$. Larger dust particles (not shown) exhibit larger ice-nucleating number fractions because ice nucleation is proportional to the particle surface area. Conen et al. (2011) showed that soil with high organic content exhibits higher IN activity than montmorillonite and postulate that ice active proteins in the soil from fragments of decaying biological material are likely the cause. The atmospheric importance of different INA materials depends not only on their ice-nucleating fractions that are shown in Fig. 5 but also on their number concentrations at cloud altitudes and the prevailing environmental conditions (e.g., temperature and humidity).

4.3.2. Observation of biological ice nuclei in the atmosphere. The plant pathogenic bacteria *Pseudomonas* are frequent in the biosphere, and *Pseudomonas* bacteria are also frequently found as airborne particles or in cloud droplets (e.g. Fuzzi et al., 1997; Amato et al., 2005, 2007a, 2007c). However, in these studies, the ice nucleation activity of the isolated *Pseudomonas* strains was not determined. Little is known about the atmospheric abundance of INA lichen and fungal spores. Pollen, for which ice nucleation activity seems to be a common property of many species, can reach peak concentrations on the order of several per litre during the pollination season (Vogel et al., 2008).

Direct observations of the involvement of biological particles in cloud ice and precipitation formation are difficult to obtain. The presence (or absence) of INA biological particles in the air, cloud condensate or precipitation can give some indications on their role in the atmosphere. Such observations are discussed in the following section.

Kumai (1961) found indirect evidence of the possible involvement of biological particles in atmospheric ice nucleation by microscopically identifying bacteria at the centre of 3 out of 307 examined snow crystals. In the pioneering studies by Maki and Willoughby (1978) and Sands et al. (1982), ice-nucleating bacteria were isolated from rain and snow. Some were even sampled at altitudes up to 2500 m above ground (Sands et al., 1982). Jayaweera and Flanagan (1982) and Lindemann et al. (1982) were the first to determine the ice nucleation activity of biological

Table 6. Compilation of laboratory measurements of the IN properties of biological particles (n.a. = data not available)

Species	Highest T,°C where INA observed	Active number fraction or active IN per unit mass at highest INA temperature	Highest observed active fraction and corresponding temperature	Freezing mode (Immersion freezing = If, Contact freezing = Ctf, Condensation freezing = Cdf)	References
Bacteria isolated from air or precipitation					
Pseudomonas fluorescens isolated from leaves, lake/stream water and/or snow	−10	0.02	0.94 (T = −16°C)	If	Maki and Willoughby (1978)
Unidentified microbacterium isolated from air above the Arctic Ocean	−4	0.05	1 (T = −18°C)	If	Jayaweera and Flanagan (1982)
Pseudomonas sp. isolated from air above the Arctic Ocean	−9	0.1	n.a.	If	Jayaweera and Flanagan (1982)
Pseudomonas syringae isolated from rain and hail	−4	n.a.	n.a.	If	Sands et al. (1982)
Pseudomonas syringae and *Erwinia herbicola* isolated from air above plant canopies and bare soil	−10	n.a.	n.a.	If	Lindemann et al. (1982)
Pseudomonas syringae isolated from air and rainwater sampled over a soybean field	−5	n.a.	n.a.	If	Constantinidou et al. (1990)
Pseudomonas sp. isolated from cloud and rain water	−21 to −29	n.a.	n.a.	If	Ahern et al. (2007)
Pseudomonas syringae isolated from rain, snow, alpine streams, lakes and wild plants	−2 to −6	10^{-7}	n.a.	If	Morris et al. (2008)
Microbacterium, *Xanthomonas*, *Bacillus*, *Acinetobacter*, *Luteimonas*, *Stenotrophomonas* and unspecified bacteria isolated from snow	−13 to −18	n.a.	n.a.	If	Mortazavi et al. (2008)
Bacteria isolated from air other habitats (list not exhaustive)					
Pseudomonas syringae	−5	$2·10^{-6}$	$5·10^{-5}$ (T = −15°C)	If	Vali et al. (1976)
Pseudomonas syringae, different strains	−5	0.0043 to 10^{-7}	n.a.	If	Gross et al. (1983)
Pseudomonas syringae strain 31R1	−1	10^{-8}	0.5 (T = −12°C)	If	Lindow et al. (1989)
Pseudomonas syringae	−8±1	0.0032	n.a.	If/Cdf	Möhler et al. (2008)
Pseudomonas viridiflava/*Pseudomonas syringae* mixture	−9.7	0.005	n.a.	If/Cdf	Möhler et al. (2008)
Pseudomonas syringae isolated from decaying alder leaves (Alnus tenuifolia)	−3	10^{-6}	0.01(T = −20°C)	If	Maki et al. (1974)
Pseudomonas sp. isolated from the guts of sub-Antarctic beetles	−3.4	10^{-6}	n.a.	If	Worland and Block (1999)
Pseudomonas Antarctica	−4	10^{-7}	0.2 (T = −10°C)	If	Obata et al. (1999)
Erwinia herbicola	−9±1	0.0007	n.a.	If/Cdf	Möhler et al. (2008)
Erwinia herbicola, cell-free centrifuged suspensions	−3	n.a.	n.a.	If	Phelps et al. (1986)
M1	−3	10^{-6}	0.01 (T = −10°C)	If	Yankofsky et al. (1981)
M1	−3	n.a.	n.a.	Ctf	Levin and Yankofsky (1983)

Table 6 (*Continued*)

Species	Highest T,°C where INA observed	Active number fraction or active IN per unit mass at highest INA temperature	Highest observed active fraction and corresponding temperature	Freezing mode (Immersion freezing = If, Contact freezing = Ctf, Condensation freezing = Cdf)	References
M1	−3	n.a.	n.a.	If	Levin and Yankofsky (1983)
Flavobacterium sp., *Psychrobacter* sp., and *Sphingomonas* sp. isolated from permafrost soil	n.a.	n.a.	$4 \cdot 10^{-7}$ (T = −10°C)	If	Ponder et al. (2005)
Snomax	−5.6	0.01	0.23 (T = −8±1°C)	If/Cdf	Möhler et al. (2008)
Snomax	−4	$1.3 \cdot 10^{12}$ g^{-1}	$5.5 \cdot 10^{12}$ g^{-1} (T = −12°C)	Cdf	Ward and DeMott (1989)
Snomax	−5.3	n.a.	n.a.	If	Wood et al. (2002)
Snomax	−26, Rhi = 116±6%	0.001–0.01	n.a.	Deposition nucleation (no experiments at warmer T)	Chernoff and Bertram (2010)
INA bacteria on oat leaves	−2.5	10^{-7}	0.008 (T < −4°C)	If	Hirano et al. (1985)
several representative Arctic and Antarctic sea-ice bacterial isolates	−40 to −42	n.a.	n.a.	If	Junge and Swanson (2008)
Lichens					
Rhizoplaca chrysoleuca (the most active of 15 investigated lichen species)	−2.3	10^{3} g^{-1}, grinded material	10^{8} g^{-1} (T = −3C), grinded material	If	Kieft (1988)
Psora decipiens (the least active of 15 investigated lichen species)	−8	10^{3} g^{-1}, grinded material	10^{5} g^{-1} (T = −12°C), grinded material	If	Kieft (1988)
18 lichen mycobionts	−4.1 to −10	n.a.	n.a.	If	Kieft and Ahmadjian (1989)
Lecanora dispersa (lichen fungus)	−4.2	$\sim 10^{4}$ g^{-1}	$\sim 7 \cdot 10^{7}$ g^{-1} (T = −8°C)	If	Kieft and Ahmadjian (1989)
Cladonia cristatella (lichen fungus)	−6.3	$\sim 10^{6}$ g^{-1}	$\sim 5 \cdot 10^{6}$ g^{-1} (T = −12°C)	If	Kieft and Ahmadjian (1989)
Ascospora fuscata (lichen fungus)	−9.1	$\sim 2 \cdot 10^{4}$ g^{-1}	$\sim 2 \cdot 10^{5}$ g^{-1} (T = −12°C)	If	Kieft and Ahmadjian (1989)
Rhizoplaca chrysoleuca (lichen fungus), different clones	−4.6 to −4.8	10^{4} to $2 \cdot 10^{5}$ g^{-1}	$\sim 2 \cdot 10^{7}$ g^{-1} (T = −12°C)	If	Kieft and Ahmadjian (1989)
13 lichen photobionts	−5.1 to −16	n.a.	n.a.	If	Kieft and Ahmadjian (1989)
Trebouxia incrustata (lichen photobiont)	−9.1	$\sim 2 \cdot 10^{4}$ g^{-1}	$\sim 6 \cdot 10^{4}$ g^{-1} (T = −12°C)	If	Kieft and Ahmadjian (1989)
Trebouxia erici (lichen photobiont)	−9.2	$\sim 6 \cdot 10^{5}$ g^{-1}	$\sim 10^{6}$ g^{-1} (T = −12°C)	If	Kieft and Ahmadjian (1989)
Trebouxia sp. (lichen photobiont)	−6	$\sim 6 \cdot 10^{4}$ g^{-1}	$\sim 10^{6}$ g^{-1} (T = −12°C)	If	Kieft and Ahmadjian (1989)
Unspecified lichen fragments from Norway, Faroe Islands, Ethiopia, UK, Australia, Antartica	−5.1	n.a.	n.a.	If	Henderson-Begg et al. (2009)
Fungi					
Penicillium digitatum spores isolated from air	−10	0.01	n.a.	If	Jayaweera and Flanagan (1982)
Cladosporium herbarum spores isolated from air	−15	0.01	n.a.	If	Jayaweera and Flanagan (1982)

Table 6 (*Continued*)

Species	Highest T,°C where INA observed	Active number fraction or active IN per unit mass at highest INA temperature	Highest observed active fraction and corresponding temperature	Freezing mode (Immersion freezing = If, Contact freezing = Ctf, Condensation freezing = Cdf)	References
Penicillium notatum spores isolated from air	−22	0.01	n.a.	If	Jayaweera and Flanagan (1982)
Penicillium frequentes spores isolated from air	−22.5	0.01	n.a.	If	Jayaweera and Flanagan (1982)
Rhizopus stolonifera spores isolated from air	−23	0.01	n.a.	If	Jayaweera and Flanagan (1982)
Fusarium avanaceum	−2.5	10^5 g^{-1}	10^{11} g^{-1} (T = − 10°C)	If	Pouleur et al. (1992)
Fusarium acuminatum	−5	n.a.	n.a.	If	Pouleur et al. (1992)
Fusarium sp. isolated from the guts of insect larvae	−5	n.a.	n.a.	If	Tsumuki et al. (1992)
Fusarium oxysporum (12 out of 42 isolates, from plants)	−1	n.a.	n.a.	If	Richard et al. (1996)
Fusarium tricinctum (8 out of 14 isolates, from plants and soil)	−1	n.a.	n.a.	If	Richard et al. (1996)
Cladosporium spores	−28.5	∼0.002	0.2 to 1 (T = − 35°C)	If	Iannone et al. (2011)
Pollen					
Pine pollen	−8	0.1	0.9 (T = − 18°C)	Cdf	Diehl et al. (2001)
Pine pollen	−16	n.a.	n.a.	If	Diehl et al. (2002)
Pine pollen	−12	n.a.	n.a.	Ctf	Diehl et al. (2002)
Birch pollen	−8	0.04	0.98 (T = − 18°C)	Cdf	Diehl et al. (2001)
Birch pollen	−10	n.a.	n.a.	If	Diehl et al. (2002)
Birch pollen	−6	n.a.	n.a.	Ctf	Diehl et al. (2002)
Oak pollen	−8	0.03	0.5 (T = − 18°C)	Cdf	Diehl et al. (2001)
Oak pollen	−14	n.a.	n.a.	If	Diehl et al. (2002)
Oak pollen	−10	n.a.	n.a.	Ctf	Diehl et al. (2002)
Grass pollen	−8	0.02	0.8 (T = − 18°C)	Cdf	Diehl et al. (2001)
Grass pollen	−14	n.a.	n.a.	If	Diehl et al. (2002)
Grass pollen	−10	n.a.	n.a.	Ctf	Diehl et al. (2002)
Alder pollen	−10	n.a.	n.a.	If	von Blohn et al. (2005)
Alder pollen	−10	n.a.	n.a.	Ctf	von Blohn et al. (2005)
Lombardy poplar pollen	−18	n.a.	n.a.	If	von Blohn et al. (2005)
Lombardy poplar pollen	−14	n.a.	n.a.	Ctf	von Blohn et al. (2005)
Redtop grass pollen	−16	n.a.	n.a.	If	von Blohn et al. (2005)
Redtop grass pollen	−16	n.a.	n.a.	Ctf	von Blohn et al. (2005)
Kentucky blue pollen	−14	n.a.	n.a.	If	von Blohn et al. (2005)
Kentucky blue pollen	−10	n.a.	n.a.	Ctf	von Blohn et al. (2005)
Various pollen, including crushed pollen	no IN observed	−	−	Deposition nucleation	Diehl et al. (2001)

Table 6 (*Continued*)

| Species	Highest T,°C where INA observed	Active number fraction or active IN per unit mass at highest INA temperature	Highest observed active fraction and corresponding temperature	Freezing mode (Immersion freezing = If, Contact freezing = Ctf, Condensation freezing = Cdf)	References
Algae					
25 algae species isolated from Antarctic soils	−5 (>-8 for 4 out of 25 species)	n.a.	n.a.	If	Worland and Lukesova (2000)
Seaweed (8 species)	−7	n.a.	n.a.	If	Lundheim (1997)
Leaf litter					
Poplar mulch	−5	$\sim 10^5 \, \text{g}^{-1}$	$\sim 5 \cdot 10^9 \, \text{g}^{-1}$ (T = − 15°C)	If	Schnell and Vali (1972)
Sage leaf litter	−6	$\sim 10^3 \, \text{g}^{-1}$	$\sim 10^7 \, \text{g}^{-1}$ (T = − 17°C)	If	Schnell and Vali (1972)
Green poplar leaves	−9	$\sim 2 \cdot 10^2 \, \text{g}^{-1}$	$\sim 2 \cdot 10^4 \, \text{g}^{-1}$ (T = − 17°C)	If	Schnell and Vali (1972)
Leaf litter of several trees and grasses in tropical climate zones	−7	$\sim 10^2 \, \text{g}^{-1}$	$\sim 4 \cdot 10^4 \, \text{g}^{-1}$ (T = − 18°C)	If	Schnell and Vali (1976)
Leaf litter of several trees and grasses in humid mesothermal climate zones	−6	$\sim 10^2 \, \text{g}^{-1}$	$\sim 4 \cdot 10^8 \, \text{g}^{-1}$ (T = − 23°C)	If	Schnell and Vali (1976)
Leaf litter of several trees and grasses in humid microthermal climate zones	−4	$\sim 10^2 \, \text{g}^{-1}$	$\sim 4 \cdot 10^{10} \, \text{g}^{-1}$ (T = − 22°C)	If	Schnell and Vali (1976)
Tea leaf litter	−5	$10^2 \, \text{g}^{-1}$	$\sim 5 \cdot 10^4 \, \text{g}^{-1}$ (T = − 12°C)	If	Schnell and Tan-Schnell (1982)
Plankton					
Cachonina Niei	−3	$10^2 \, \text{g}^{-1}$	~ 1 (T = − 14°C); $10^6 \, \text{g}^{-1}$ (T = − 10°C)	If	Schnell (1975)
Ochromonus danica and *Porphyridium aerugineum*	> − 15	n.a.	n.a.	If	Schnell (1975)
Unspecified mixture of 95% phytoplankton, 5% zooplankton and associated debris	−3.5	$10^2 \, \text{g}^{-1}$	$10^6 \, \text{g}^{-1}$ (T = − 10°C)	If	Schnell and Vali (1975)
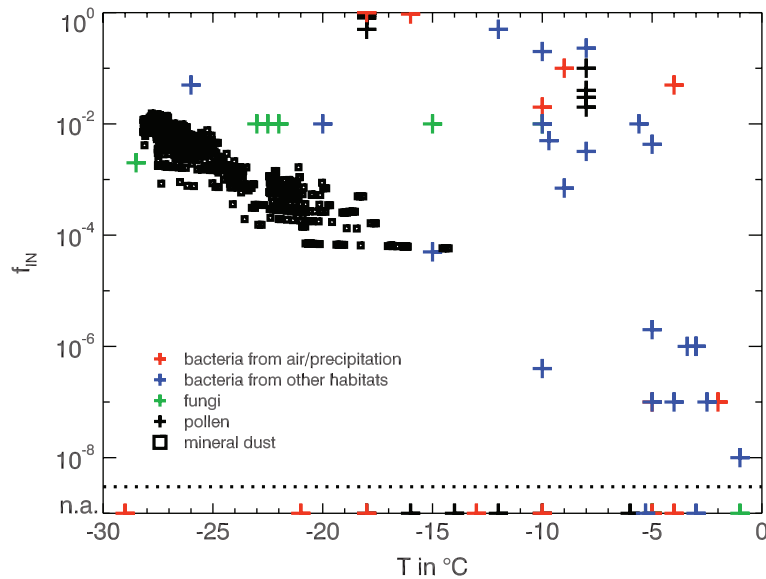
Fig. 5. Ice nucleating number fraction f_{IN} at the observed IN onset and maximum activity temperatures from the experiments listed in Table 6. For comparison, f_{IN} data for immersion freezing on mineral dust (natural soil samples, median diameters of 0.2–1 µm) are included (M. Niemand, personal communication).

particles sampled directly from the atmosphere. In the Arctic, two types of bacteria (an unidentified strain and a *Pseudomonas* strain) and five fungal spores were observed with moderate to high ice nucleation activity (Jayaweera and Flanagan, 1982). Lindemann et al. (1982) found significant concentrations of INA bacteria at 10°C above different plant canopies and bare soil and identified them as *Pseudomonas syringae* and *Erwinia herbicola*. The INA bacteria accounted for 0–4% of the total bacteria. Constantinidou et al. (1990) isolated *Pseudomonas syringae* from rainwater and aerosol samples over a soy bean field and tested them as INA at −5°C. Recently, Morris et al. (2008) studied *Pseudomonas syringae* strains isolated from rain, snow, alpine streams, lakes and wild plants and found that all the strains isolated from snow showed ice nucleation activity at −2 to −5°C, while this property was rare among the other strains. However, other samples of bacteria isolated from precipitation exhibited only moderate ice nucleation activity (Ahern et al., 2007; Mortazavi et al., 2008).

Christner et al. (2008a, b) demonstrated that snow and rain samples from around the world contain ice nuclei active at temperatures above −10°C. A majority of these ice nuclei was found to be inactivated through heat treatment (at 95°C) and/or lysozyme digestion, indicating a probable bacterial and/or proteinaceous origin. The observed concentrations of warm-temperature ice nuclei ranged between below 10 and several hundred per litre of snow/rain water, which is much lower than the estimated numbers of hydrometers per litre precipitation (Diehl and

Wurzler, 2010; Hoose et al., 2010a). Ice nuclei sampled from the urban atmosphere (Henderson-Begg et al., 2009), which were also active at temperatures above −10°C, were not deactivated by lysozyme treatment and heating to 60°C (but by heating to 90°C). This was interpreted as an indication that these ice nuclei were not bacterial, but rather from lichen or fungi. Also, ice nuclei concentrations at 10°C in air and snow at a high-elevation mountain site did not correlate with the relative abundances of well-known INA bacteria species such as *Pseudomonas syringae* and *Erwinia herbicola* (Bowers et al., 2009). It was suggested that ice nucleation at this site was due to other bacterial species, varying expression of the bacterial ice-nucleation capacities, or other biological particles.

It can be expected that biological ice nuclei are particularly abundant in regions with active vegetation. Prenni et al. (2009) investigated aerosol particles sampled above the canopy in the Amazon forest and inferred that the majority of the ice nuclei at −25°C and warmer were of biological origin (but absolute concentrations of ice nuclei at these temperatures were low, on the order of 1–2 l^{-1}). Ice nuclei at colder temperatures were in large part contributed by mineral dust. At cirrus cloud altitude, Pratt et al. (2009) observed a case of co-occurrence of biological material with mineral dust after long-range transport: From mass-spectroscopic measurements of ice crystal residues in wave clouds, 50% mineral dust particles and 33% biological particles were identified. But, only in one out of many research flights was a measurable fraction of biological material observed.

In summary, the presently available observations do not give a consistent picture. The strongest indications of ice-nucleation activity in clouds are available for bacterial or fungal ice nucleators. Quantitative measurements are unfortunately rare and cover only anecdotal events. In particular, more studies quantifying the atmospheric concentrations of INA biological particles in comparison to other ice-nucleating agents, such as mineral dust and soot, would be desirable.

4.3.3. Modelling of biological ice nuclei. Numerical simulations of the effects biological ice nuclei in clouds began with Levin et al. (1987), who studied the efficiency of cloud seeding with INA bacteria for precipitation enhancement in a 1.5-dimensional cloud model. Later, Diehl and Wurzler (2004); Diehl et al. (2006) parameterised freezing of droplets containing or colliding with unknown amounts of different biological ice nucleators for a parcel model with detailed microphysics. In a follow-up study (Diehl and Wurzler, 2010), the freezing rates were scaled with typical fractions of droplets containing bacteria, mineral dust and soot particles, respectively, and it was shown that typical bacteria concentrations yielded much lower ice crystal concentrations than typical mineral dust concentrations. Ariya et al. (2009), in studies with a 1.5-dimensional model of a convective cloud, and employing INA biological aerosol concentrations of less than $1\,l^{-1}$, pointed out that even such low IN concentrations can trigger cloud glaciation through ice-multiplication processes. The comprehensive empirical ice nucleation parameterisation by Phillips et al. (2008) includes biological material as part of the 'insoluble organic' particles. In a cloud-system resolving model, cloud micro- and macrophysical properties, including precipitation, were sensitive to variations of the 'insoluble organic' aerosol by a factor of 100 (Phillips et al., 2009). The first global model studies of the impact of biological particles by Hoose et al. (2010a), Hoose et al. (2010b) used simple emission parameterisations for bacteria, fungal spores and pollens to simulate their concentration in the atmosphere. The freezing rates were derived from classical nucleation theory and laboratory data (Chen et al., 2008a). The average contribution of biological particles to heterogeneous ice nucleation in mixed-phase clouds (integrated over all temperature regions in the troposphere) was calculated to be only 0.00001%, with an uppermost estimate of 0.6%. Instead, atmospheric ice nucleation was found to be dominated by mineral dust, which is also in agreement with recent observations (Choi et al., 2010; DeMott and Prenni, 2010; DeMott et al., 2010; Klein et al., 2010). The contribution of biological particles to ice nucleation in relatively warm cloud layers (above $-10°C$) might be higher but was not quantified in these studies.

In summary, the effect of biological particles as ice nuclei on clouds and precipitation is strongly dependent on the atmospheric concentrations of INA species. Most likely, these concentrations exhibit strong temporal and spatial variations, and any effect on clouds is therefore likely seasonal and local in nature. However, more quantitative observations of INA biological particles in the atmosphere are necessary to allow better estimates of their effects on clouds.

4.4. Optical properties

The absorption and scattering of radiation by aerosol particles are important physical properties that influence regional and global radiation budgets. Better understanding of the effect that natural aerosols have on the atmosphere is necessary to constrain effects that anthropogenic influence may have on global climate. Because PBAP can be a major fraction of aerosol number and surface area in certain locations, it is possible that they may also affect climate forcing both directly (by absorbing or scattering radiation) and indirectly (through cloud processes). Certain fungal spores and other PBAP classes can be highly coloured and absorbing, which may increase their direct influence on the surrounding atmosphere (e.g. Adams et al., 1968; Troutt and Levetin, 2001). However, there have been very few studies estimating the direct effect of PBAP on climate, in part because geographically or temporally comprehensive PBAP measurements are not yet available. A theoretical description of the interaction between electromagnetic radiation and PBAP is difficult because the Mie theory is only valid for spheres, and thus many biological aerosol particles cannot be well described (Bohren and Huffman, 1983).

Some work has been done to directly measure certain optical properties of PBAP that could be relevant to the investigation of atmospheric aerosol. Spankuch et al. (2000) showed that down-welling infrared flux was significantly increased when pine pollen concentrations were higher, suggesting that emissions of certain pollens may cause localised atmospheric warming events. Several groups have shown that pollen can cause visible coronae around the sun and moon and could therefore influence local solar radiation properties (Parviainen et al., 1994; Trankle and Mielke, 1994; Mims, 1998; Schneider and Vollmer, 2005).

Most work involving the optical properties of PBAP has used detailed physical measurements in the laboratory and, as such, has only limited obvious application to the atmosphere at large. Surbek et al. (2009) characterised the elastic light scattering of a number of pollen species. Several groups have made detailed measurements of the polarisation and scattering properties specific to bacteria

and other biological aerosol types (Bickel et al., 1976 and references therein; Bohren and Huffman, 1983; Vandemerwe et al., 1989). Gurton et al. (2001) measured infrared extinction by bacterial spores. Harding and Johnson (1984) measured quasi-elastic light scattering, and Gittins et al. (1999) measured infrared absorption of *Bacillus subtilis* bacteria. Yabushita and Wada (1985) performed IR and UV absorption measurements of *E. coli* and yeast organisms.

In view of the much higher abundance of mineral dust discussed by Hoose et al. (2010b), the influence of biological material on aerosol optical properties may be relatively small on global scales. However, on regional scales PBAP may sometimes have a substantial influence on the total scattering and absorption of light by aerosols. Using chemical tracers and multivariate statistical analysis, Guyon et al. (2004) showed that up to 66% of aerosol mass and 47% of the light absorption in air over the Amazon Rainforest were attributable to biogenic particles during the wet season. During the wet-to-dry transition period, biogenic particles still accounted for up to 35% of light absorption, even though there was already a substantial amount of biomass burning aerosol present. These results are consistent with many earlier measurements (e.g. Artaxo et al., 1988, 1998), which showed that biogenic aerosol makes up a large fraction of the Amazonian aerosol mass burden, especially in the coarse fraction. In the absence of definitive identification, earlier studies assumed that it consisted mostly of PBAP (Andreae and Crutzen, 1997). This was confirmed with less uncertainty using multiple techniques by Pöschl et al. (2010), who showed that PBAP accounted for $\sim 67\%$ of the aerosol mass (or volume) of all particle sizes sampled above the rainforest in a remote section of Amazonia, Brazil during a time period of very low influence from airborne mineral dust or anthropogenic pollution. In addition, biological organisms or material may often be attached to mineral dust particles and might also influence the optical properties of these combined particles. Thus, PBAP need to be considered when modelling local and regional optical properties above and downwind of biologically active regions. Additional direct atmospheric measurements of light absorption and scattering by biogenic particles will likely be necessary to help provide suitable model inputs and such measurements are strongly recommended.

5. Conclusions and outlook

Scientific investigations of biological aerosol particles in the atmosphere have a long history going back to the nineteenth century. Since then, the topic has attracted attention in various different research areas. In the last decade, there has been a surge in interest within the atmospheric community based partly on the development of new measurement techniques and on studies indicating that PBAP may play an important role as ice nuclei influencing the formation of clouds and precipitation.

Depending on the character of the biological particle of interest, as well as on the scope of the scientific questions asked, manifold methods are available to study PBAP. Thus, we have included an overview of current methods for sampling and analysis of biological aerosols including traditional and modern techniques.

Further studies of biological aerosols will lead to a better understanding of their role in climate and atmospheric processes and will also help to improve understanding of their impacts on humans. Recently developed and emerging techniques for sampling and analysing airborne biological particles have bolstered efforts to understand the properties of ambient PBAP. However, for better comparison among different datasets, sampling and analysis techniques have to be standardised. Efficient and reliable analytical techniques must be developed for the identification and quantification of PBAP as well as for the determination of the abundance and diversity of PBAP and their seasonal variation on regional and global scales (atmospheric biogeography).

One of the main influences of PBAP on climate and atmosphere is through the capability of certain PBAP to function as excellent ice nuclei. Future research should thus concentrate on the determination of actual emission rates and optical properties of PBAP and to link results from laboratory experiments concerning the IN ability of PBAP to atmospheric measurements.

Global modelling is one of the rising methods to track and understand the worldwide global distribution of PBAP. Atmospheric models can estimate the atmospheric effects of IN active biological aerosol particles on clouds and help identify targets for experimental research. However, the models need to be constrained and confirmed by experimental data. Future research should use field and laboratory data to better constrain numerical models of PBAP sources, their transformation in the atmosphere and effects on climate. An important task is the delivery of larger and more comprehensive datasets from sampling sites worldwide and their incorporation into atmospheric models, to ground model efforts in a solid empirical foundation.

6. Acknowledgements

7. Appendix

AMS	Aerodyne Mass Spectrometer
ATOFMS	TSI Aerosol Time-of-Flight Mass Spectrometer
ATP	Adenosine Triphosphate
BAMS	Bioaerosol Mass Spectrometry
Bp	Base Pairs
BS	Break-Down Spectroscopy
CCN	Cloud Condensation Nuclei
CFU	Colony Forming Units
DAPI	4.6-diamidino-2-phenylindole
ddNTP	dideoxynucleotidetriphophate
DNA	Deoxyribonucleic Acid
dNTP	deoxynucleotidetriphosphate
EPS	Exopolymer Secretions
FBAP	Fluorescent Biological Aerosol Particles
FISH	Fluorescent in-situ hybridization
GF	Growth Factor
Hulis	Humic Like Substances
IN	Ice Nuclei
INA	Ice Nucleation Active
IPCC	Intergovernmental panel on climate change
ISI	Institute for Scientific Information
ITS	Internal Transcribed Spacer
LDD	Long Distance Dispersal
LIBS	Laser-Induced Breakdown Spectroscopy
LIDAR	LIght Detection And Ranging
MALDI-TOF	Matrix-Assisted Laser Desorption Ionization Time-of-Flight
MS	Mass Spectrometry
NCBI	National Center for Biotechnology Information
OC	Organic Carbon
PBAP	Primary Biological Aerosol Particles
PCR	Polymerase Chain Reaction
PIXE	Particle-Induced x-ray Emission
PM	Patriculate Matter
RH	Relative Humidity
RNA	Ribonucleic Acid
rRNA	Ribosomal RNA
SEM	Scanning Electron Microscopy
SIBS	Spark-Induced Breakdown Spectroscopy
SOA	Secondary Organic Aerosol
STXM	Scanning Transmission X-ray Microscopy with Near-Edge X-ray Absorption Fine Structure
TIRFM	Total Internal Reflection Fluorescence Microscopy
T-RFLP	Terminal Restriction Fragment Length Polymorphism
TSP	Total Suspended Particles
UV	Ultraviolet Light
UV-APS	Ultraviolet Aerodynamic Particle Sizer
WIBS	Wide Issue Bioaerosol Spectrometer

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