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Microbiology and atmospheric processes: an upcoming era of research on bio-meteorology

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Abstract

For the past 200 years, the field of aerobiology has explored the abundance, diversity, survival and transport of micro-organisms in the atmosphere. Micro-organisms have been explored as passive and severely stressed riders of atmospheric transport systems. Recently, an interest in the active roles of these micro-organisms has emerged along with proposals that the atmosphere is a global biome for microbial metabolic activity and perhaps even multiplication. As part of a series of papers on the sources, distribution and roles in atmospheric processes of biological particles in the atmosphere, here we describe the pertinence of questions relating to the potential roles that air-borne micro-organisms might play in meteorological phenomena. For the upcoming era of research on the role of air-borne micro-organisms in meteorological phenomena, one important challenge is to go beyond descriptions of abundance of micro-organisms in the atmosphere toward an understanding of their dynamics in terms of both biological and physico-chemical properties and of the relevant transport processes at different scales. Another challenge is to develop this understanding under contexts pertinent to their potential role in processes related to atmospheric chemistry, the formation of clouds, precipitation and radiative forcing. This will require truly interdisciplinary approaches involving collaborators from the biological and physical sciences, from disciplines as disparate as agronomy, microbial genetics and atmosphere physics, for example.

1 Introduction

The presence of micro-organisms in the atmosphere was revealed by the clever experiments of Spallanzani in the middle of the 18th century (Capanna, 1999) and of Pasteur at the end of the 19th century (Pasteur, 1890). Yet, the atmosphere still presents a frontier for pioneering microbiologists. Aside from classical pursuits of aerobiology (descriptions of the abundance and diversity of micro-organisms in the atmosphere,

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of their response to the physical-chemical conditions of the atmosphere and of their dissemination), questions relative to the atmosphere as a habitat for micro-organisms have been little explored. Furthermore, for decades, microbiologists and atmosphere physicists and chemists have suspected that air-borne micro-organisms play roles in atmospheric processes. But these roles have not yet been clearly elucidated. This paper will present an overview of atmospheric microbiology, the possibility of an “atmosphere biome” as a distinct global ecosystem and the pertinence of a range of new questions about the role of micro-organisms in atmospheric processes. It will also set the stage for several other related review and perspectives papers in this issue that will present specific conceptual and technical challenges in detail. Although this paper covers the potential role of micro-organisms per se, biological particles at large are likely to play many of the roles evoked here.

With the growing awareness of climate changes on our planet, interest in atmospheric processes that define climate has heightened and diversified thereby bringing new attention to the possible roles of micro-organisms in these processes. In 2006, the European Science Foundation funded an exploratory workshop on “Microbiological Meteorology” convened at the French National Agronomic Research Institute (INRA) in Avignon (Morris and Sands, 2006). The objective of the workshop was to bring together the necessary competence to examine the interplay between vegetation, bio-aerosols, atmospheric processes and air quality. The twenty attendees represented the disparate fields of agronomy, atmosphere physics and chemistry, bioclimatology, environmental modeling, meteorology, microbiology and plant pathology. We worked to create an initial momentum for new interdisciplinary research programs around questions of the impact of micro-organisms on atmospheric processes. As part of this momentum, we have requested the dedication of this special issue of Biogeosciences to “Properties of biological aerosols and their impact on atmospheric processes”, and are presenting herein our collective ideas on research needs to enhance the emergence of interdisciplinary collaboration on exciting and novel questions.

What are some of the potential roles for micro-organisms in atmospheric processes

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and what interdisciplinary research might be required to elucidate their roles? If considered as inert particles, microbial cells as well as other types of biological particles can have properties that allow them to act as cloud condensation nuclei (Ariya and Amyot, 2004) and to participate in radiative forcing (Jaenicke, 2005). Some also produce highly active ice nuclei that may be involved in processes that lead to precipitation (Ariya and Amyot, 2004, Morris et al., 2004, Szyrmer and Zawadzki, 1997). This question is treated in detail in another paper of this special issue (Möhler et al., 2007). In addition, many air-borne micro-organisms likely metabolizes chemical components of aerosols thereby modifying atmosphere chemistry (Ariya and Amyot, 2004, Ariya et al., 2002). Moreover, non-metabolic pathways for chemical modification due to the existence of biological particles are also theoretically feasible. For instance, desorption of molecules from biological surfaces (Cote et al., 2007), chemical release due to cell lysis, and collision-coalescence processes all can modify the chemical composition of atmospheric gas-phase and particulate matters. It should be noted that chemical reactions dictate the lifetime of atmospheric particles, their ability to act as cloud condensation nuclei and/or ice nuclei, as well as the production of atmospheric oxidants. This is because physical chemistry governs the total mass of airborne particles, their acidity, the amount of light they scatter and absorb, their reactivity, and their ability to act as cloud condensation nuclei. It can be argued that many of these effects could be studied simply from the perspective of the physical sciences via classical approaches used for other types of aerosols. However, micro-organisms are metabolically active with dynamic biological properties, and many microbial cells maintain viability in the atmosphere. Hence, the microbial traits that lead to the potential effects on the atmosphere listed above are due to properties of cells that vary with changes in metabolism, in gene expression, in the distribution of charges across the cell wall, and in other myriad cellular characteristics that are environmentally induced and as cells mature and senesce. Understanding the mechanisms and dynamics of their variable states is the domain of microbiologists. Micro-organisms are nature's product. Air-borne dissemination is likely to be a natural and necessary part of the life cycle of many micro-organisms

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that has occurred since their emergence on this planet. Dispersal via the atmosphere thus plays a central role in concepts of microbial biogeography such as distance-decay or taxa-area relationships (Green and Bohannan, 2006). In the evolutionary history of micro-organisms, adaptation to conditions in the atmosphere has likely had a consequence on microbial population genetics and genome structure. The importance of selection pressures related to the interplay of micro-organisms with atmospheric conditions and processes for the evolutionary history of micro-organisms is an open field for novel research. Among the different sources of micro-organisms in the atmosphere, plants in particular make an important contribution. A role for agronomists and plant biologists in elucidating mechanisms of emission of micro-organisms into the atmosphere, their dissemination and ultimate fate clearly points to the need for interdisciplinary research.

2 Biological aerosol particles are omnipresent in the atmosphere

For the past 200 years, research in the field of aerobiology has focused primarily on describing the types and taxonomic groups of biological particles in the atmosphere and the spatio-temporal variations in their abundance. The year 1847 can be considered as the starting point of aerobiology in a relatively modern sense when Ehrenberg published his monograph on “Passat dust and blood rain – a great invisible organic action and life in the atmosphere” (Krumbein, 1995). By 1849 figures had been published with detailed pictures of particles, especially biological particles including pollen, spores and fragments of organisms (Ehrenberg, 1849). Interest eventually shifted to the micro-organisms in the air. Scientific associations on aerobiology were founded and books and articles published (Edmonds and Benninghoff, 1973; Gregory, 1961). On the other hand, the newly emerging field of air chemistry (Junge, 1963) did not even mention the presence of biological particles in the air. The main reason might be that micro-organisms are counted as particles per m^3 , while atmospheric particles in general are numbered in the tens of thousands per cm^3 . The exclusion of

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biological particles has been perpetuated in discussions of air chemistry and climate (WMO/UNEP, 2001). In a recent appeal to “put the challenge back into aerobiology”, scientists in this field suggest intensifying the study of aerial movement of biological particles, and standardizing monitoring techniques and expanding monitoring networks to improve forecasting movement of biota important particularly to agriculture and human health (Comtois and Isard, 1999). The questions we envision on the frontier of aerobiology today encompass but go beyond the needs of a census.

In 1993, an IGAP (International Global Aerosol Program) workshop in Geneva defined primary biological aerosol particles as airborne solid particles (dead or alive) that are or were derived from living organisms, including micro-organisms and fragments of all varieties of living things. According to the recent work of Jaenicke (Jaenicke, 2005) about 25% of the particles suspended in air (by mass or number) are primary biological aerosol particles. This estimate is based on numerous observations, mainly via staining methods to distinguish individual protein-containing particles from others. In other work, particles smaller than 2 μm have been distinguished by morphology as well as typical elements (Matthias-Maser and Jaenicke, 1991). Other estimates are presented in Table 1. Over the Amazon, it is not surprising that 74% of the aerosol volume (or mass) consists of biological particles (Table 1). However, the presence of about 20% world-wide is surprising. The data summarized here does not include the Polar Regions, where large numbers of ice particles are re-suspended from the surface, and where each ice particle contains a cloud condensation nucleus. It is likely that up to 25% of those nuclei consist of biological particles. According to recent estimates, among the naturally present ice nucleators in fresh snow collected from diverse geographical sites, over 100 of these particles per L are of biological origin (Christner et al., 2008) and might indicate the nature of ice nucleators in the atmosphere. This abundance of biological particles in the air certainly raises the question of the world-wide production of such particles. Jaenicke (Jaenicke, 2005) has estimated that the major sources of particles in Earth’s atmosphere – desert, oceans, and the biosphere – are of equal strength. But, the importance of organisms as a component of aerosols

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and as players in atmospheric physico-chemical processes is likely to vary substantially under different environmental conditions given that there is important spatial and temporal variability of quantities of micro-organisms in the air (Bauer et al., 2002, Ross et al., 2003, Sattler et al., 2001).

5 The clear take-home message from two centuries of investigations is that biological particles in the atmosphere are omnipresent. Micro-organisms are a dominant component of these biological particles. Among the bacteria detected in the atmosphere, the majority is Gram-positive and many are spore-formers such as *Bacillus* sp. *Bacillus* and *Microbacterium* spp. were particularly dominant in the air during a dust event (Kellogg and Griffin, 2006). But Gram-negative bacteria, having a cell wall that is considered to be more fragile than that of Gram-positive bacteria, have also been found (Lighthart, 1997). Among the fungi, spores similar to those from *Cladosporium*, *Aspergillaceae*, *Alternaria*, *Botrytis*, and various Basidiomycetes (*Coprinus*, *Ustilago*) have been frequently observed in the atmosphere (Gregory, 1961; Kellogg and Griffin, 10 2006), but spores of *Cladosporium* spp. seem to be numerically the most dominant. Viruses have also been observed in the atmosphere, in particular in aerosols over the sea surface (Aller and Kusnetsova, 2005) and in clouds (Castello et al., 1995), and virus-like particles have been reported to be associated with transoceanic dust (Griffin et al., 2001).

20 Special mention should be made of *Pseudomonas syringae*. This Gram-negative plant pathogenic bacterium is not the most abundant of the micro-organisms present in the atmosphere (Lighthart, 1997), but it will very likely become one of the most highly studied organisms with regard to potential impact on atmospheric processes. This is due in particular to its well-known activity as an ice nucleator at temperatures near zero (reviewed by Morris and collaborators (Morris et al., 2004)), and to its significant upward flux in the atmosphere (Lindemann et al., 1982), its presence in clouds (Amato et al., 2007; Sands et al., 1982), its potential activity as a cloud condensation nucleus (Snider et al., 1985), and recent observations about its abundance in snow and rain (Morris et al., 2008). Furthermore, all strains of *P. syringae* isolated from snow and 25

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rain by Morris and colleagues were ice nucleation active at temperatures between -2° and -6° whereas not all strains of this bacterium isolated from various other substrates (including plants, water and epilithic biofilms) were active as ice nucleators (Morris et al., 2008). A few other species of plant-associated bacteria (including *Xanthomonas* sp., *Pantoea agglomerans*, and other *Pseudomonas* spp.) as well as the plant associated fungus *Fusarium avenaceum* (Pouleur et al., 1992) are known to be ice nucleation active but very little, relative to *P. syringae*, is known about their abundance in the atmosphere. Amato and co-workers have recently reported the isolation of *F. avenaceum* from clouds at about 1450 m altitude (Amato et al., 2007) in central France. Algae are also known to be readily disseminated in the air and a few species are ice nucleation active at temperatures as warm as -6°C (Worland and Lukesova, 2000). But there have been no studies on the presence of ice nucleation active algal species in the atmosphere. However, several authors have argued that algae and other microbes may play an active role in the atmosphere, for instance in ice nucleation and precipitation (Ariya and Amyot, 2004; Hamilton and Lenton, 1998; Möhler et al., 2007; Morris et al., 2004; Szyrmer and Zawadzki, 1997).

This qualitative and quantitative information about biological aerosols is, nevertheless, subject to variation as a function of altitude, region (rural, urban, forest, ocean, etc.) and climatic factors (temperature, relative humidity, rainfall, wind, etc). Furthermore, it has been known for quite some time that micro-organisms, and in particular fungal spores and bacteria, can be present up to high altitudes – between 1 and 7 km above the Earth's surface (for a review see Gregory, 1961). But more recently it was suggested that altitude has an effect on the composition of the air spora and that there is a particular "alpine type" of air microflora (Ebner et al., 1989). A distinct phylogenetic signature of airborne bacteria found in snow cover has been observed in a high alpine station, leading Alfreider and colleagues (Alfreider et al., 1996) to propose a dominant role of the atmosphere in the dispersal of bacteria. Land use (urban vs. rural land, or different degrees of urbanization) also has an impact on the occurrence of spores and daily concentration in the air (Calderon et al., 1997; Kasprzyk and Worek, 2006).

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The most prevailing and well-studied effects on air flora variability are those due to meteorological factors such as wind speed and direction, relative humidity, rainfall and solar radiation (Jones and Harrison, 2004). The chemical composition and pH of aerosols can also influence microflora in the air. Several authors have reviewed the influence of meteorological factors on bacteria, fungi and pollen in the atmosphere (Jones and Harrison 2004; Lighthart and Shaffer 1997). The abundance of fungi in the air and the taxonomic groups represented in an outdoor sampling campaign conducted in Turin, Italy depended on the temperature, relative humidity and rainfall (Marchisio et al., 1997). The abundance of *Alternaria* and *Cladosporium* spp. in the air has also been reported to vary with different bioclimatic conditions (Rodriguez-Rajo et al., 2005). In a study of the abundance of viable spores of the plant pathogenic fungus *Gibberella zeae* at 60 m above the ground, more viable spores were detected under cloudy than under clear conditions, but fewer were found during rainfall (Maldonado-Ramirez et al., 2005) presumably because they were washed out. The role of sandstorms in disseminating fungi, bacteria and pollen via the air has been reviewed (Kellogg and Griffin, 2006). The daily concentrations of air-borne bacteria and fungal spores at sampling sites in mid-ocean were significantly correlated with daily desert dust concentration in the air (Griffin et al., 2006). Moreover, the composition of the air flora in terms of certain fungal spores can vary considerably during the dust transport episodes (Wu and Tsai, 2004). Concerning the chemical composition of the atmosphere, air-borne microbial concentrations have been observed to increase with increasing atmospheric CO₂ concentrations (Klironomos et al., 1997). According to the authors of that study, this phenomenon is probably linked to the increase of spore production on substrates with increasing CO₂ concentrations. The pH in the atmosphere can also influence the abundance and types of microflora present. In clouds, an acidic pH favors the presence of fungi and spore-forming bacteria whereas a neutral pH is favourable to the presence of a greater diversity of micro-organisms (Amato et al., 2005).

Seasonal and daily variation in the amount and kinds of micro-organisms in the air is also remarkable. High concentrations of air-borne bacteria and fungal spores

frequently occur from spring to fall in temperate areas of the world, mainly due to the fact that leaf surfaces are a major source of fungi (Levetin and Dorsey, 2006; Mitakakis et al., 2001) and bacteria (Tong and Lighthart, 2000) in the air. The higher concentrations of bacteria observed in the summer (July–August) over two agricultural sites in Oregon (USA) may reflect the flux from agricultural sources and activities and dry dusty soil conditions at this time of the year (Tong and Lighthart, 2000). Even on the scale of a single day, the air-borne spore concentration increased from 20 000 spores/m³ to 170 000 spores/m³ in a 2-h period in the area around Tulsa, Oklahoma (USA) (Burch and Levetin, 2002). Diurnal periodicity has also been observed (Lindemann and Upper, 1985; Tong and Lighthart, 2000). On the other hand, for the fungus *Gibberella zeae*, no differences were observed in air-borne concentrations between the day and night at 60 m above the ground (Maldonado-Ramirez et al., 2005).

3 Atmospheric transportation of biological particles

The mechanisms that contribute to the abundance and ubiquity of micro-organisms in the atmosphere are the foundation of the roles they can play in atmospheric processes. Via these mechanisms, sufficient numbers of micro-organisms can be transported to the pertinent atmospheric sites. These mechanisms include those related to emission from the various sources, transport in the atmosphere and deposition. The mechanisms of microbial survival in the atmosphere are also critical to atmospheric processes requiring active metabolism. Aside from discharge of fungal spores from conidiophores or from turgid structures such as asci (Jones and Harrison, 2004), very little is known about emission mechanisms, particularly for bacteria. As a consequence, we do not sufficiently understand the mechanisms underlying source strength. Likewise, the little information available about the properties of particles transporting micro-organisms, and again particularly for bacteria, leaves us wondering about how micro-organisms survive, the factors that contribute to their metabolic activity in the atmosphere, and the most appropriate values for particle parameters in models to estimate their trajectories.

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Above water surfaces, creation of aerosols containing micro-organisms occurs by bubble bursting. This can lead to biological particles in the atmosphere in remote regions such as above the central Arctic Ocean (Leck and Bigg, 2005). On land, aerial parts of plants are considered a principal source of air-borne micro-organisms (Lighthart, 1997). Creation of aerosols containing micro-organisms that inhabit plant surfaces is likely due to wind stress that might directly lift micro-organism or via secondary impacts due to wind stress-induced deformations of leaves. Drying of leaf surfaces due to biological processes or to changing atmospheric conditions could also enhance the emission of biological particles. We can speculate that micro-organisms might also be released into the atmosphere even under calm conditions if microbial growth leads to population sizes that exceed the physical carrying capacity of the plant surface. These mechanisms might be compounded by changes in the charge of leaf surfaces during the day that would modify attraction or repulsion of biological particles (Leach, 1987).

Understanding mechanisms of emission is linked to our capacity to measure flux above suspected sources and in relation to changing conditions thought to influence emission. Flux measurements are also a basic variable in models to predict coincidence of sufficient particle load and atmospheric conditions that contribute to atmospheric processes. Calculation of microbial flux requires measurements of microbial particle concentration at several heights combined with estimations of latent heat flux. Measurement of particle concentration and physico-chemical characterization are among the major challenges that have been pre-occupying aerobiology since its inception. Bioaerosols include a wide range of organic matter with a large degree of variability in physical and chemical characteristics such as size, shape, phase, composition, structure, solubility, volatility, hygroscopicity and surface properties. These aerosols can be single spores, pollen, bacteria and viruses; aggregates; and products and by-products of, or attached to non biological particles (Sun and Ariya, 2006). Common techniques for measurement of aerosol number density, shape, optical and surface properties, as well as chemical characterization of condensed and semi-volatile matter

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have been deployed, but none can fully capture the physical and chemical complexity of biological matter. Several tools available to environmental microbiologists have also been widely used in sampling and analysis of biological aerosols. To date, existing measurement techniques are tailored towards the applications and goals that vary significantly from one domain of research to another thereby leaving room for much needed complementarity of physical-chemical and biological analyses. In this paper, we intensify the challenge of measuring particle numbers and properties by raising questions of the appropriate properties of biological particles to be used as counters. Clearly, measurements of total biological particle concentration, or viable microbial concentration, or concentration of a single species of interest will only lead us part of the way to the estimates needed. Concomitant measures of occurrence of microbial particles with their capacity as, for example, condensation or ice nuclei, or as binding sites or metabolic sinks for various atmospheric chemicals will be needed. There is a need to determine which particle properties are most relevant. Techniques are needed that allow detection over space and relatively short time intervals of these particles, whose concentrations are likely to be low. The development of in situ bioaerosol analyzers with a wide dynamic range is highly desirable to avoid the shortcomings associated with sampling. Presently most sampling techniques have analytical biases affecting detection, characterization, mobility and versatility, and potential contamination, whereas the existing in situ methods are unable to capture detailed chemical characteristics at sufficient detection limits.

Much of the data concerning the abundance of specific micro-organisms in the air (such as the fungi and bacteria cited above) are based on the growth of these organisms on the culture media used for sampling. This approach has hidden the nature of the particles with which these micro-organisms are associated. From direct observation of air-borne particles, we know that fungi in the atmosphere may be present as single spores or clusters (Aylor and Ferrandino, 1985, Bainbridge and Stedman, 1979, Pinkerton et al., 1998). For bacteria, size-graded samples from Andersen spore samplers, for example, indicate that a large proportion of viable air-borne bacteria are

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associated with particles that are much larger than the size of single bacterial cells (Lighthart, 1997). Observations of clusters containing bacterial-like particles and in some cases covered with mucus-like material (Leck and Bigg, 2005; Lighthart, 1997) support the suggestion that chunks or remnants of microbial biofilms might be a sort of sailing ship for bacteria offering both a means of take-off and survival in the air (Morris and Monier, 2003). But overall, too little is known about the properties of particles that transport micro-organisms in the air. Specific information on the size and nature of the microbe-carrying particles is essential for transport models dependent on parameters concerning aerodynamic properties of particles and is also important for the development of detection tools that capture or detect particles based on size, shape, phase and chemical characteristics. Currently, only a very limited number of model developments and applications deal with atmosphere transport or biological particles (Helbig et al., 2004; Isard et al., 2005; Pasken and Pietrowicz, 2005; Sofiev et al., 2006). These models suffer from a lack of experimental data that allow parameterization of emission fluxes and of other processes which biological particles undergo during transport.

4 Consolidating microbiology and atmospheric sciences in the upcoming era of bio-meteorology

Research on the role of micro-organisms in meteorological phenomena and in atmospheric processes in general is part of a growing interest in the importance of the biosphere on climate change. This is an under-explored component of a research field referred to as bio-meteorology. An important challenge for the next decades regarding micro-organisms is to go beyond descriptions of microbial abundance in the atmosphere toward an understanding of their dynamics in terms of both biological and physico-chemical properties and of the relevant transport processes at different scales. Specific examples of unresolved questions in this regard are listed in the text above. Other examples are also presented in the other review papers in this issue. An additional challenge is to develop this understanding under contexts pertinent to

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their potential role in atmospheric processes thereby providing support for their specific involvement in these processes. This can implicate construction of conceptual and numerical models of microbial flux into the environment; of trajectories, survival, multiplication; metabolic activity and perhaps even genetic exchange; and of the degree to which different species or physiological states of micro-organisms mediate processes affecting atmospheric chemistry, the formation of clouds, precipitation and radiative forcing. Sattler, Puxbaum and Psenner (Sattler et al., 2001) who found active bacteria in supercooled cloud droplets, and Daniel Jacob (Dept. Earth and Planetary Sciences, Harvard Univ., personal communication) considered possible implications of bacteria as sources of oxygenated organics in the atmosphere with implications for HO_x radical chemistry and organic aerosol formation. The role of airborne bacteria as potential sources and sinks for acetone and other volatile organics in the atmosphere is one of the interesting questions in microbial meteorology, with implications for climate and weather. In the face of the foreseen climate changes, an important goal of future research would be to quantify the extent to which micro-organisms are involved in atmospheric processes that could mitigate the undesirable foreseen changes and to predict how human activities might enhance some of these processes. For some microbial species we may discover that the negative roles with which they are identified today (plant pathogens, for example) are counterbalanced by beneficial roles in the atmosphere thereby bringing into question the need for new approaches to managing these microbial populations in the environment that account for both of these seemingly opposing roles.

This research will require truly interdisciplinary collaboration both in the laboratory and in the field. Students trained in both the physical and biological sciences will bridge the gap among senior scientists from different disciplines. Currently, few students take the risk to attain this multiple competency in their training because the extra investment in coursework is not always readily compatible with the requirements and the time constraints imposed by their training program. A greater flexibility of training programs in this regard will enhance progress of this and other research themes in environmental

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sciences. Coordinated sampling campaigns at multiple field sites will also be needed. This will likely require some sort of coordinating body or a well-orchestrated consortium of laboratories. Finally, advances in numerical models concerning cloud microphysics to air pollution at local, regional and global scales could aid this effort. During the last three decades sophisticated numerical models for a variety of atmospheric scales have been developed. This includes very detailed models with a high spatial and temporal resolution and with detailed microphysics. Corresponding chemistry and aerosol modules have been developed. Some models permit the study of interactions of cloud physics and aerosol physics including chemistry. Although there has been a major leap in the development of numerical models, there are still major gaps in these models for properly capturing elemental physical and chemical processes such as aerosol-cloud interactions. This has been noted as a major uncertainty for predicting climate change. Furthermore, only a very limited number of model applications deal with biological particles, their sources and their possible environmental implications. Extensive modelling that is complementary to field and laboratory multi-disciplinary studies of bioaerosols is needed.

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Table 1. Cellular fraction in atmospheric aerosols by number. The fraction by mass is roughly the same (Gruber and Jaenicke, 1999; Gruber et al., 1999; Jaenicke et al., 2000; Matthias-Maser and Obolkin, 2000; Matthias-Maser et al., 1995; White et al., 1999).

Location	Cellular fraction by number, $r > 0.2 \mu\text{m}$	Reference
Helgoland	15.3%	(Gruber et al., 1999)
North Sea (3000 m altitude)	15%	(Gruber et al., 1999)
Mainz	23.7%	(Matthias-Maser et al., 1995)
Southern Atlantic Ocean	16.7%	(Matthias-Maser et al., 1995)
Baikal, Siberia	20%	(personal communication, T. Khodzer, Russian Academy of Sci., Irkutsk)
Jungfraujoch (3500 m altitude)	13.1%	(Matthias-Maser et al., 2000)
Mace Head, Ireland	30% (continent) 40% (marine)	(Jennings et al., 1999)
Balbina, Amazon	74% (by volume)	(Graham et al., 2003)

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