Aerobiologia (2013) 29:153–159
DOI 10.1007/s10453-012-9259-x

BRIEF COMMUNICATION

Total bacterial number concentration in free tropospheric air above the Alps

Y. Xia · F. Conen · C. Alewell

Received: 21 July 2011 / Accepted: 11 April 2012 / Published online: 28 April 2012

Abstract Over a period from June to October 2010, we carried out four short campaigns on the northern alpine ridge (High Altitude Research Station Jungfraujoch, 3,450 m above sea level) to determine bacterial number concentrations by collecting aerosol with liquid impingers, followed by filtration, fluorescent staining and counting with a microscope. Impinger liquid was also subjected to drop freeze tests to determine the number of ice nucleators. Parallel measurements of ^{222}Rn enabled us to distinguish air masses with no, or little, recent land surface contact (free troposphere, $^{222}Rn \leq 0.50$ Bq m^{-3}) from air masses influenced by recent contact with land surface ($^{222}Rn > 0.50$ Bq m^{-3}). In free tropospheric air, concentration of total bacteria was on average 3.4×10^4 cells m^{-3} (SD $= 0.8 \times 10^4$ cells m^{-3}). When wind conditions preceding sampling were calm, or when the station was in clouds during sampling, there was no detectable difference in bacterial number concentrations between free tropospheric air and air influenced by recent land surface contact. One campaign was preceded by a storm. Here, recent land surface contact had enriched the air in bacterial cells (up to 7.5×10^4 cells m^{-3}). Very few of these bacteria may act as ice nucleators in clouds. The median ratio of ice nucleators to the number of bacterial cells in our study was 1.0×10^{-5}. We conclude that injection of bacterial cells into the free troposphere is an intermittent process. Conditions controlling the release of bacteria into near surface air are probably more of a limiting factor than vertical transport and mixing of near surface air into the free troposphere.

Keywords Total bacterial number concentration · Free troposphere · Radon · Ice nucleator

1 Introduction

Bacteria are omnipresent in the atmosphere (Jaenicke et al. 2007). In a recent study, it was indicated that "…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 microorganisms in these processes" (Morris et al. 2011). Among the roles, the ice-nucleating activity of some bacteria catches particular attention because of a potential impact on cloud formation and development of precipitation (Yankofsky et al. 1981; Morris et al. 2005; Möhler et al. 2007; Christner et al. 2008). Plant canopies provide large surfaces for bacterial growth and are major sources of airborne bacteria, while bare soils are supposed to play a minor one (Lindemann et al. 1982). Growth of bacterial communities on surfaces depends on moisture, temperature, substrate

Y. Xia (✉) · F. Conen · C. Alewell
Institute of Environmental Geosciences, University of Basel, Bernoullistrasse 30, 4056 Basel, Switzerland
e-mail: yxrain@gmail.com

availability and other environmental factors (Harrison et al. 2005). Release into the atmosphere is largely driven by wind speed (Jones and Harrison 2004). Among those released, biological particles of 0.2−10 μm size have long atmospheric residence times. Particles in this range may remain airborne for several days to a few weeks (Raes et al. 2000). Thus, they can be transported with air currents over long distances (Prospero et al. 2005). They are removed from the atmosphere slowly by dry deposition or, much faster, by wet deposition.

Concentrations of total bacteria at high altitudes are of interest from a meteorological point of view. In snowfall, a large proportion of ice nucleators active at temperatures warmer than −10°C have been found to be intact bacterial cells (Christner et al. 2008), but also dead cells and even cell fragments may act as condensation and ice nuclei in clouds (Möhler et al. 2008). Direct measurements of total bacterial cell concentrations at a height where clouds can develop are rare (Bauer et al. 2002). Most observations were made in lowlands within a few metres of the land surface. Historically, they have focused on the concentration of cultivable bacteria, sometimes misleadingly referred to as viable bacteria. However, concentrations of cultivable bacteria are two or three orders of magnitude smaller in comparison with concentrations of total bacteria (Chi and Li 2007). Estimating total from cultivable cell numbers is impossible because the cultivable proportion depends on meteorological factors, such as temperature and UV radiation (Chi and Li 2007). The sum of all investigations to date shows that mean concentrations of total bacteria in ambient air are likely to be generally larger than 1×10^4 cells m^{-3} over land. Over sea they tend to be 2–3 orders of magnitude lower than over land (Burrows et al. 2009). Estimates of concentrations at greater altitudes in the atmosphere are based on a combination of surface observations and atmospheric transport modelling (Hoose et al. 2010a). Our objective was to directly determine bacterial cell number concentrations at a greater height, where the atmosphere is dominated by air masses with no, or little, recent contact with the land surface, in the so-called free troposphere. Such air masses are characterised by low concentrations of ^{222}Rn, a radioactive noble gas (half-life time = 3.8 days) emitted naturally from all land surfaces. A second, minor objective was to determine the number of ice nucleators active at temperatures ≥−10 °C in these air masses.

2 Materials and methods

Sampling was carried out at the High Altitude Research Station Jungfraujoch (7°59′E, 46°33′N; 3,450 m above sea level) in the Swiss Alps. The station is part of the Global Atmosphere Watch Program of the World Meteorological Organization (GAW/WMO). One 4-day, two 3-day and one 1-day campaign were carried out between June and October 2010, including the measurement of weather conditions (Table 1).

For total bacterial number concentrations, a single sampling event consisted of collecting aerosol during a 3-h period with a liquid impinger (BioSampler; SKC, Inc.). In previous tests at the station, we found no measurable change in sampling efficiency over such a prolonged period, as long as we added sterile H_2O to the collectors at 30-min intervals to maintain a constant volume of liquid. Air was aspired through a 4 cm diameter, 50 cm length, glass tube from outside the station. A mesh (1 mm) at the tube inlet prevented entry of insects or other larger particles. Prior to sampling, the liquid impinger was washed with ethanol and sterilised in dry heat (1 h at 220 °C). It was then filled with 20 ml of 0.1 M tetrasodium PP_i dispersant (Kepner and Pratt 1994). The flow rate during sampling was maintained at 0.75 m^3 h^{-1}. After collection, the sample was fixed with formalin (2% (vol/vol) final concentration). All liquids were filtered through a 0.2-μm-pore-size filter prior to use. Blank samples were prepared with the same equipment and procedures, except that no air was passed through the dispersant liquid. Bacteria fixed with formalin were captured within 1 h after sampling by microfiltration through a 0.2-μm-pore-size, 25-mm, black polycarbonate membrane filter (Millipore, Isopore) placed in a glass vacuum filter funnel unit (Sartorius Stedim Biotech GmbH) equipped with a custom built inlay to reduce the effective filter area to a diameter of 6 mm. Pressure difference across the filter during sampling was maintained at 100 mbar. Glass funnel and filter holder were sterilised prior to use by the same procedure as the liquid impinger. Until analysis within less than a week, the filter was kept at −20 °C. For analysis, it was stained for 10 min with

Table 1 Results of four campaigns to measure total bacterial cell number, ice nuclei active at temperatures ≥−10 °C and ^{222}Rn activity concentrations at the High Altitude Research Station Jungfraujoch (3,450 m above sea level). Time stamps are at the end of 3 hour measurement intervals and are in local time (UTC + 2). Values in brackets indicate 1 standard error

Campaign	Date	Time	Relative humidity (%)	Air temperature (°C)	Wind speed (m/s)	Sky	Wind direction	^{222}Rn (Bq m^{-3})	Bacteria (in 10^4 m^{-3})	Ice nuclei active ≥−10 °C (m^{-3})
A	22.06.2010	11:00	11–13	−2.8	2.8	Clear	NW	0.50	2.1 (±0.2)	0.0
		18:00	9–13	1.3	4.2	Clear		0.44	3.0 (±0.5)	0.4
	23.06.2010	11:00	16–29	0.4	3.3	Clear		0.68	–	–
		18:00	17–24	3.9	2.5	Clear		1.05	3.3 (±0.4)	0.0
	24.06.2010	11:00	20–21	−0.5	3.3	Clear		0.41	3.9 (±0.3)	0.9
		18:00	42–98	0.2	3.8	Clear		1.22	–	–
	25.06.2010	11:00	31–32	−0.7	1.8	Clear		0.52	3.5 (±0.4)	2.3
		18:00	42–95	2.2	1.1	Clear		1.43	3.9 (±0.3)	0.4
B	20.07.2010	11:00	30–37	3.9	4.5	Clear	SE	0.30	2.5 (±0.2)	1.8
		18:00	46–75	6.9	0.7	Clear		1.22	4.0 (±0.3)	1.4
		21:00	75–81	5.7	0.3	Heavy fog		2.70	2.3 (±0.2)	2.8
	21.07.2010	11:00	79–86	3.5	4.6	Heavy fog		3.23	3.1 (±0.6)	0.0
		18:00	71–92	5.7	3.4	Heavy fog		3.68	3.9 (±0.4)	3.8
		21:00	76–92	4.2	2.3	Heavy fog		3.71	3.0 (±0.4)	1.8
	22.07.2010	11:00	94–100	2.0	9.2	Heavy fog		2.46	4.3 (±0.3)	0.0
		18:00	96–100	3.1	8.3	Heavy fog		2.63	3.9 (±0.2)	0.9
		21:00	99–100	2.3	6.0	Heavy fog		2.69	2.2 (±0.4)	3.8
C	01.09.2010	11:00	57–60	−5.0	7.1	Clear	NW	0.40	3.7 (±0.4)	0.0
		18:00	58–64	−1.4	4.8	Clear		0.34	3.8 (±0.5)	0.4
		21:00	64–67	−1.7	4.9	Clear		0.38	4.6 (±0.5)	0.4
D	06.10.2010	11:00	9–67	1.4	1.7	Clear	NW and SE	0.35	3.7 (±0.3)	0.0
		18:00	54–63	3.6	0.8	Clear		0.37	3.7 (±0.5)	0.0
		21:00	50–65	1.9	3.3	Clear		0.58	4.0 (±0.5)	0.4
	07.10.2010	11:00	41–46	1.2	4.0	Clear		0.31	3.1 (±0.2)	0.0
		18:00	40–68	3.1	2.3	Clear		0.64	3.9 (±0.2)	1.4
		21:00	48–75	1.2	4.7	Clear		1.04	7.5 (±0.9)	0.0
	08.10.2010	11:00	69–77	0.6	2.9	Clear		0.69	3.5 (±0.3)	0.0
		18:00	57–87	2.0	1.3	Clear		0.94	4.6 (±0.4)	0.4
		21:00	78–91	0.1	2.7	Clear		1.16	5.8 (±0.4)	0.0

4′,6-diamidino-2-phenylindole (DAPI), a DNA binding dye at a final concentration of 0.01% (wt/vol). The filter was mounted on a glass slide, and bacterial cells, identified by size and shape, were counted with a fluorescence microscope (Leica DM2500) equipped with a 100 W high-pressure mercury lamp, a 100× ocular lens, a 460-nm filter and an objective with 10 × 10 10-μm grids. Total cell numbers were determined since no distinction can be made between live and dead cells with the stain we used. Ten microscope fields were selected on the filter by turning the microscope stage randomly without watching the microscope. The counting for one filter was finished within 30 min before the fluorescence started fading. The total number of bacterial cells m^{-3} (N) was calculated as:

$$N = \frac{M \times A_f}{V} \quad (1)$$

where M represents the average number of bacteria per field count (typically between 20 and 50), A_f the ratio of effective area of the filter to the area of the counting grid, V the volume of sampled air (m^3 at local pressure and temperature). Blank counts were about one order of magnitude smaller than sample counts. The standard error of N was determined by the standard deviation of numbers counted in the ten fields on each slide divided by the square root of ten. In addition to bacteria, it would have been interesting to also determine the abundance of spores or pollen, as was done by Wiedinmyer et al. (2009) for samples from Storm Peak Laboratory in Colorado (3,200 m above sea level). However, the number of large particles on our slides was too small to provide reliable values. In addition, the few large particles we occasionally saw under the microscope were not clearly identifiable by their morphology.

For determining the number of ice nucleators active at temperatures ≥ -10 °C, a second impinger was operated as described before, but the sample was not fixed with formaldehyde. The sampling liquid from the impinger was split into 0.3 ml portions, transferred into 0.5-ml Eppendorf safe lock tubes. These were exposed to decreasing temperatures (-6 to -10 °C) in a water bath cooling at a rate of 1 °C in 3 min. The number of frozen tubes was inspected visually after each cooling step. Numbers of ice nucleators at each temperature step were calculated according to Vali (1971). After this analysis, the safe lock tubes were put into a boiling water bath for 10 min to denature and deactivate all biological ice nucleators (Christner et al. 2008). Heat-treated samples were analysed again in the cooling water bath to check for the presence of non-biological ice nucleators that would not be destroyed by heating. Additional measurements were taken with blank samples consisting of the same liquid, but where no air has been passed through. None of the blank samples did freeze at ≥ -10 °C.

Since 2008, we operate a 700-litre volume, dual-loop, two-filter ^{222}Rn detector (Whittlestone and Zahorowski 1998) at the station. Half-hourly ^{222}Rn activity data provided by the detector were averaged over the same 3-h period as the liquid impingers were operated. Statistical counting error over a 3-h period with this instrument at 0.50 Bq m^{-3} is 3 %. Since 2009, we operate a second such detector on the roof of the Physics Institute at the University of Bern, in the foreland of the Alps, 580 m above sea level and 60 km North-West of the High Altitude Research Station Jungfraujoch. Analysis of data from both detectors has shown us that air with recent land surface contact had no, or little, influence on air masses at Jungfraujoch when ^{222}Rn values at Jungfraujoch were $\leq$0.50 Bq m^{-3}. In 90 % of such situations, ^{222}Rn concentrations near the land surface (at Bern) were more than 5.4 times larger than those at Jungfraujoch, indicating very poor vertical transport from lower altitudes to the High Altitude Research Station Jungfraujoch. Therefore, we presume our bacterial cell number measurements are taken in free tropospheric air when ^{222}Rn values at Jungfraujoch are $\leq$0.50 Bq m^{-3}.

3 Results and discussions

3.1 Bacterial number concentrations

The days before the first campaign in June the station was at times clear, at times in clouds, intermittently affected by frost and experiencing snowfall. At the beginning of the campaign, atmospheric pressure had increased and wind speeds had decreased. Free tropospheric air (^{222}Rn = 0.44 –0.50 Bq m^{-3}) surrounded the station during the first day, and bacterial number concentrations were $\leq 3 \times 10^4$ cells m^{-3} (Table 1). Days 2 to 4 of the campaign saw ^{222}Rn concentrations increase several-fold during afternoons and return to values around 0.5 Bq m^{-3} the following mornings. So, air arriving in the afternoon was influenced by air that had recent contact with the land surface, hence its enrichment in ^{222}Rn. However, bacterial cell number concentrations did not change measurably. This may have been caused by wet surfaces and low wind speeds in the lowlands during this campaign, preventing larger numbers of cells from becoming airborne from their habitats near the land surface.

During the campaign in July, the weather situation was variable. Initially clear skies were clouding in the first evening of our sample collection on 20 June. Average relative humidity increased from 30 to 81 % the first day. Heavy fog enclosed the whole Jungfraujoch region with low visibility until the end of this

campaign. Relative humidity remained high between 71 and 100 %. High pressure dominated the station site. Free tropospheric air (0.30 Bq m^{-3}) influenced the station during the morning of the first day. Coincident total bacterial number concentration was 2.5×10^4 m^{-3}. In the afternoon of the same day, air influenced by recent land surface contact moved up to the station (1.22 Bq m^{-3}) with increased bacterial number concentrations (4.0×10^4 m^{-3}). When heavy fogs enclosed the station in the evening, the changes in ^{222}Rn and bacterial number concentrations did no longer follow the same pattern. ^{222}Rn concentration more than doubled, while bacterial number concentration was reduced almost to half the value in the afternoon. Although ^{222}Rn concentrations remained 2 to 3 times higher during days 2 and 3, bacterial number concentrations were on average smaller (3.2×10^4 m^{-3}) during the same period compared to the clear afternoon of the first day (20 June, 18:00). During foggy conditions, upward moving bacterial cells may have been intercepted and removed by wet deposition before reaching station altitude.

The short campaign in September was characterised by cold and moist air and free tropospheric background conditions prevailed. ^{222}Rn concentrations remained low ($\leq$0.40 Bq m^{-3}). Bacterial number concentrations were around 4.0×10^4 m^{-3}. Combined with the samples from free tropospheric air during the other three campaigns, we estimate that the background number concentration of total bacteria in free tropospheric air (^{222}Rn $\leq$ 0.50 Bq m^{-3}) above the Alpine region during summer and early autumn was around 3.4×10^4 cells m^{-3} (SD = 0.8×10^4 cells m^{-3}). This is larger than the total bacterial number concentrations reported for out-of-cloud samples at Mt. Rax (1,644 m a.s.l.) in the Austrian Alps. These were in a range from 6.7×10^3 to 1.9×10^4 cells m^{-3} (Bauer et al. 2002). This small concentration of bacterial cells at Mt. Rax may be due to the snow cover during the campaign effectively suppressing emission of bacterial cells into the atmosphere. A recent atmospheric simulation study estimates a zonal average of 10^3 to 10^4 cells m^{-3} for the latitude and pressure where Jungfraujoch station is located (Hoose et al. 2010a). This estimate is likely to be a lower limit in comparison with our values because it includes air at these altitudes above land and sea, and concentrations above sea are much lower than above most land surfaces (Burrows et al. 2009). Furthermore, we conducted our campaigns during the growing period for vegetation, when concentrations are expected to be larger than during winter (Burrows et al. 2009).

Sampling in October was preceded by a storm in the lowlands as well as at the station itself. Previously, when boundary layer air had influenced the station (campaigns in June and July), mean hourly wind speeds during the 3 days preceding the campaign, and during the campaign itself, were generally <10 m s^{-1} and on average around 4 m s^{-1}. On the evening of 03 October, wind speeds began to exceed 10 m s^{-1}, reached values around 20 m s^{-1} by the middle of the following day and returned to values <10 m s^{-1} only on 05 October early morning. Wind direction alternated between NW and SE. At the beginning of the campaign on 06 October, atmospheric pressure increased and wind speed had further decreased. During the entire campaign period, the station experienced clear skies. Free tropospheric air in the morning and afternoon of the first day (0.35–0.37 Bq m^{-3}) became slightly enriched by air with recent land surface contact towards later the evening (0.58 Bq m^{-3}). Bacterial number concentrations also increased slightly during the first evening. The following morning, bacterial number and ^{222}Rn concentrations were both back to smaller values. From there on, both parameters continued to increase and decrease in synchrony until the end of the campaign. Unlike our previous observations, there was a significant correlation ($r = 0.81$; $p = 0.008$) between bacterial number and ^{222}Rn activity concentrations during the 3 days of this campaign. This demonstrates a clear enrichment of air near the land surface in bacterial cells compared to the free tropospheric background. In the earlier campaigns, there was no significant difference ($p = 0.47$) in bacterial number concentrations between free tropospheric air (3.4×10^4 m^{-3}) and boundary layer air (3.4×10^4 m^{-3}). In this campaign, air with recent land surface contact (>0.50 Bq m^{-3}) had average bacterial number concentrations of 4.9×10^4 m^{-3}, significantly larger ($p = 0.04$) than in free tropospheric air (3.5×10^4 m^{-3}). High wind speeds during the storm preceding the campaign had probably led to an increased release of bacteria from the surfaces they grew on and enriched near surface air with bacterial cells. Because of the long residence time of bacteria-sized particles in the atmosphere (Raes et al. 2000), near surface air remained enriched with

bacterial cells for several days following the storm. Such air was then transported during the campaign up to the station in the afternoon and evenings when vertical atmospheric mixing was strongest. Wind speed has been found to have a significant positive influence on bacterial number concentrations in air in previous studies. Lindemann and Upper (1985), making measurements over a plot of snap beans, found that bacterial number concentrations and upward flux correlated positively with wind speed and that there was no upward bacterial cell flux when wind speed was less than 1 m s^{-1}. Di Giorgio et al. (1995) also found that bacterial number concentrations increased with wind speed. Turnbull et al. (1998) observed airborne bacteria downwind from point sources only in strong wind conditions.

3.2 Number concentrations of ice nucleators

A minor second objective of this study was to determine numbers of ice nucleators active at temperatures ≥ -10 °C in the same air masses. Hoose et al. (2010b) presumed that about 1 in 10^5 bacterial cells in the atmosphere may have ice-nucleating properties. During a 3-h sampling period with an air flow rate of 0.75 m^3 h^{-1}, we collected on average less than a total of 10^5 cells. Hence, we could expect to find at best a few ice nucleators in each sample. Consequently, the precision of our measurement was low. In 11 of the 27 samples, not a single ice nucleus was detected at temperatures ≥ -10 °C. In three samples, a single ice nucleus was active at −7 °C, equivalent to 0.4 m^{-3}. The largest numbers of ice nucleators active at −10 °C or warmer (up to 3.8 m^{-3}) were found when the station was in heavy fog (Table 1). Average numbers of ice nucleators active at ≥ -10 °C were significantly larger ($p = 0.04$) in heavy fog (1.9 m^{-3}) than under clear sky conditions (0.5 m^{-3}). At a similar high altitude station (Storm Peak Laboratory, 40°27′N, 106°44′W, 3,200 m above sea level), Bowers et al. (2009) found also larger numbers of ice nucleators in cloudy, compared to clear, air. The median ratio of ice nucleators to the number of bacterial cells in our study was 1.0×10^{-5}, so exactly the value presumed by Hoose et al. (2010b) and within the range observed by Bowers et al. (2009). All ice nucleators we detected at temperatures ≥ -10 °C were of biological origin. It has to be mentioned that these ice nucleators may have also been other than bacterial cells. Biological residues other than bacterial cells could also have contributed to the ice active nucleators (Conen et al. 2011). Consequently, the proportion of ice nucleation active bacteria in our samples may have even been smaller than 1.0×10^{-5}. Our measurements were taken during the warmer part of the year. Number concentrations of ice nucleators active ≥ -10 °C are likely to be larger during winter and early spring, when phenotypic expression of ice nucleation is favoured by cold temperatures (Ruggles et al. 1993).

4 Conclusions

Timing of our campaigns concentrated on fair weather conditions. Consequently, our results only cover a narrow range of weather situations occurring throughout a year. Parallel measurements of ^{222}Rn activity concentration allowed us to distinguish between conditions when the station was in free tropospheric air, and when air with recent surface contact influenced the station. Concentrations of total bacteria in free tropospheric air were fairly constant, on average around 3.4×10^4 cells m^{-3} (SD = 0.8×10^4 cells m^{-3}). Admixture of air masses with recent land surface contact into free tropospheric air, as reflected by increased ^{222}Rn activity, did not always increase bacterial cell number concentrations at higher altitude. Markedly, it did so after a storm event, when more bacterial cells will have become airborne into near surface air than under calm conditions. We conclude that the injection of bacterial cells into air at higher altitudes must be an intermittent process. Conditions controlling the release of bacteria into near surface air are probably more of a limiting factor to bacterial number concentrations at higher altitudes than vertical transport of near surface air to higher altitudes. The number of ice nucleators active at ≥ -10 °C is five orders of magnitude smaller the number of bacterial cells in free tropospheric air above the Alps.

Acknowledgments This project was funded by the Swiss National Science Foundation (project no. 200020-117622/1). Further financial support was provided by the Freiwillige Akademische Gesellschaft Basel. We are grateful to Wlodek Zahorowski, Australian Nuclear Science and Technology Organisation, for providing the ^{222}Rn detectors and supporting their continued upgrade and operation. We thank the International Foundation High Altitude Research Stations

Jungfraujoch and Gornergrat (HFSJG), 3012 Bern, Switzerland, for providing the infrastructure and making it possible for us to work at the High Altitude Research Station at Jungfraujoch. In particular, we like to thank the custodians of the High Altitude Research Station Jungfraujoch for hospitality and support.

References

Bauer, H., Kasper-Giebl, A., Löflund, M., Giebl, H., Hitzenberger, R., Zibuschka, F., et al. (2002). The contribution of bacteria and fungal spores to the organic carbon content of cloud water, precipitation and aerosols. *Atmospheric Research, 64*, 109–119.

Bowers, R. M., Lauber, C. L., Wiedinmyer, C., Hamady, M., Hallar, A. G., Fall, R., et al. (2009). Characterization of airborne microbial communities at a high-elevation site and their potential to act as atmospheric ice nuclei. *Applied and Environmental Microbiology, 75*, 5121–5130.

Burrows, S. M., Elbert, W., Lawrence, M. G., & Pöschl, U. (2009). Bacteria in the global atmosphere—Part 1: Review and synthesis of literature data for different ecosystems. *Atmospheric Chemistry and Physics, 9*, 9263–9280.

Chi, M. C., & Li, C. S. (2007). Fluorochrome in monitoring atmospheric bioaerosol and correlations with meteorological factors and air pollution. *Aerosol Science and Technology, 41*, 672–678.

Christner, B. C., Morris, C. E., Foreman, C. M., Cai, R., & Sands, D. C. (2008). Ubiquity of biological ice nucleators in snowfall. *Science, 319*, 1214.

Conen, F., Morris, C., Leifeld, J., Yakutin, M. V., & Alewell, C. (2011). Biological residues define the ice nucleation properties of soil dust. *Atmospheric Chemistry and Physics, 11*, 9643–9648.

Di Giorgio, C., Krempff, A., Guiraud, H., Binder, P., Tiret, C., & Dumenil, G. (1995). Atmospheric pollution by airborne microorganisms in the city of Marseilles. *Atmospheric Environment, 30*, 155–160.

Harrison, R. M., Jones, A. M., Biggins, P. D., Pomeroy, N., Cox, C. S., Kidd, S. P., et al. (2005). Climate factors influencing bacterial count in background air samples. *International Journal of Biometeorology, 49*(3), 167–178.

Hoose, C., Kristjansson, J. E., & Burrows, S. M. (2010a). How important is biological ice nucleation in clouds on a global scale? *Environmental Research Letters, 5*, 024009. doi: 10.1088/1748-9326/5/2/024009.

Hoose, C., Kristjansson, J. E., Chen, J. P., & Hazra, A. (2010b). A classical-theory-based parameterization of heterogeneous ice nucleation by mineral dust, soot and biological particles in a global climate model. *Journal of Atmospheric Science, 67*, 2483–2503.

Jaenicke, R., Matthias-Maser, S., & Gruber, S. (2007). Omnipresence of biological material in the atmosphere. *Environmental Chemistry, 4*(4), 217–220.

Jones, A. M., & Harrison, R. M. (2004). The effects of meteorological factors on atmospheric bioaerosol concentrations—A review. *Science of the Total Environment, 326*(1), 151–180.

Kepner, R. L., Jr, & Pratt, J. R. (1994). Use of fluorochromes for direct enumeration of total bacteria in environmental samples: Past and present. *Microbiological Reviews, 58*, 603–615.

Lindemann, J., Constantinidou, H., Barchet, W., & Upper, C. (1982). Plants as sources of airborne bacteria, including ice nucleation-active bacteria. *Applied and Environmental Microbiology, 44*, 1059–1063.

Lindemann, J., & Upper, C. D. (1985). Aerial dispersal of epiphytic bacteria over bean plants. *Applied and Environment Microbiology, 50*, 1229–1232.

Möhler, O., DeMott, P. J., Vali, G., & Levin, Z. (2007). Microbiology and atmospheric processes: The role of biological particles in cloud physics. *Biogeosciences, 4*, 1059–1071.

Möhler, O., Georgakopoulos, D. C., Morris, C. E., Benz, S., Ebert, V., Hunsmann, S., et al. (2008). Heterogeneous ice nucleation activity of bacteria: New laboratory experiments at simulated could conditions. *Biogeosciences, 5*, 1425–1435.

Morris, C. E., Georgakpoulos, D., & Sands, D. (2005). Ice nucleation active bacteria and their potential role in precipitation. *Journal de Physique IV France, 121*, 87–103.

Morris, C. E., Sands, D. C., Bardin, M., Jaenicke, R., Vogel, B., Leyronas, C., et al. (2011). Microbiology and atmospheric processes: Research challenges concerning the impact of airborne micro-organisms on the atmosphere and climate. *Biogeosciences, 8*, 17–25.

Prospero, J. M., Blades, E., Mathison, G., & Naidu, R. (2005). Interhemispheric transport of viable fungi and bacteria from Africa to the Caribbean with soil dust. *Aerobiologia, 21*, 1–19.

Raes, F., Dingenen, R. V., Vignati, E., Wilson, J., Putaud, J. P., Seinfeld, J. H., et al. (2000). Formation and cycling of aerosols in the global troposphere. *Atmospheric Environment, 34*, 4215–4240.

Ruggles, J. A., Nemecek-Marshall, M., & Fall, R. (1993). Kinetics of appearance and disappearance of classes of bacterial ice nuclei support an aggregation model for ice nucleus assembly. *Journal of Bacteriology, 175*, 7216–7221.

Turnbull, P. C. B., Lindeque, P. M., Le Roux, J., Bennett, A. M., & Parks, S. R. (1998). Airborne movement of anthrax spores from carcass sites in the Etosha National Park, Namibia. *Journal of Applied Microbiology, 84*, 667–676.

Vali, G. (1971). Quantitative evaluation of experimental results on heterogeneous freezing nucleation of supercooled liquids. *Journal of Atmospheric Science, 28*, 402–409.

Whittlestone, S., & Zahorowski, W. (1998). Baseline radon detectors for shipboard use: Development and deployment in the first aerosol characterisation experiment ACE-1. *Journal of Geophysical Research, 103*(16), 743–751.

Wiedinmyer, C., Bowers, R. M., Fierer, N., Horanyi, E., Hannigan, M., Hallar, A. G., et al. (2009). The contribution of biological particles to observed particulate organic carbon at a remote high altitude site. *Atmospheric Environment, 43*, 4278–4282.

Yankofsky, S. A., Levin, Z., Bertold, T., & Sandlerman, N. (1981). Some basic characteristics of bacterial freezing nuclei. *Journal of Applied Meteorology, 20*, 1013–1019.