Modelling the impact of fungal spore ice nuclei on clouds and precipitation

Ana Sesartic1, Ulrike Lohmann1 and Trude Storelvmo2

1 ETH Zurich, Institute for Atmospheric and Climate Science, 8092 Zurich, Switzerland
2 Department of Geology and Geophysics, Yale University, New Haven, CT, USA

E-mail: ana.sesartic@env.ethz.ch

Received 2 January 2013
Accepted for publication 14 February 2013
Published 27 February 2013
Online at stacks.iop.org/ERL/8/014029

Abstract
Some fungal spore species have been found in laboratory studies to be very efficient ice nuclei. However, their potential impact on clouds and precipitation is not well known and needs to be investigated. Fungal spores as a new aerosol species were introduced into the global climate model (GCM) ECHAM5-HAM. The inclusion of fungal spores acting as ice nuclei in a GCM leads to only minor changes in cloud formation and precipitation on a global level; however, changes in the liquid water path and ice water path as well as stratiform precipitation can be observed in the boreal regions where tundra and forests act as sources of fungal spores. Although fungal spores contribute to heterogeneous freezing, their impact is reduced by their low numbers as compared to other heterogeneous ice nuclei.

Keywords: bioaerosol, fungi, aerosol–cloud interactions

1. Introduction

Fungal spores are part of the atmospheric bioaerosols which also comprise particles such as pollen, bacteria or viruses. Interest in bioaerosols is mainly related to their health effects, impacts on agriculture, ice nucleation and cloud droplet activation and atmospheric chemistry (Morris et al 2011). In the present study, the focus lies on fungal aerosols and the modelling of their emission, transport and impacts on cloud microphysics.

Griffin (2001, 2006) and Prospero et al (2005) showed that fungal spores can be transported over long distances before being deposited either due to gravity, wash out by rain or impaction (Gregory 1967). Furthermore, Jaenicke et al (2007) and Huffman et al (2012) among others found that fungal spores are a major contributor to the bioaerosol mass in the Amazon basin, while simulations conducted by Heald and Spracklen (2009) came to the conclusion that 23% of all primary emissions of organic aerosol are of fungal origin.

The research on ice nucleation activity of fungal spores and lichen is still in its beginning, however it has been found that some fungal spores can act as very effective ice nucleators. Lichen were found to nucleate ice at temperatures of −8 °C or higher (Kieft 1988, Kieft and Ruscetti 1990). The fungal species Fusarium avenaceum and Fusarium acuminatum (Pouleur et al 1992) also produce highly effective ice nuclei (IN) with a nucleating activity comparable to that of the well known IN bacterium Pseudomonas sp. (Pouleur et al 1992). In contrast to those findings, Iannone et al (2011) observed a poor ice nucleation ability of Cladosporium spores, with immersion freezing starting only at −28.5 °C. This might be due to the spore surface being coated with hydrophobic proteins that are widespread in filamentous fungi such as Cladosporium sp.

Recent field measurements have highlighted the possible importance of bioaerosols as ice nucleators in the atmosphere (Pratt et al 2009, Prenni et al 2009). Recent findings by Huffman et al (2013) indicate that rainfall can trigger intense bursts of bioparticle emission and massive enhancements of atmospheric bioaerosol concentrations by an order of
Following Stier et al (2005) the standard deviation is constant and set to $\sigma = 1.59$ for the nucleation, Aitken, and accumulation modes and to $\sigma = 2.00$ for the coarse and bioaerosol modes.

| Modes   | Size range ($\mu m$) | Mixed/soluble | Insoluble |
|---------|----------------------|---------------|-----------|
| Nucleation | $r \leq 0.005$     | $SO_2$        | —         |
| Aitken  | $0.005 < r \leq 0.05$ | $SO_2$, BC, OC | BC, OC    |
| Accumulation | $0.05 < r \leq 0.5$ | $SO_2$, BC, OC, SS, DU | DU       |
| Coarse  | $0.5 < r \leq 1$    | $SO_2$, BC, OC, SS, DU | DU       |
| Bioaerosol | $1 < r$             | $SO_2$, BC, OC, SS, DU, BCT, FNG | DU, BCT, FNG |

magnitude or more. Spores acting as ice nuclei might influence cloud and precipitation formation processes, as has already been proposed by Morris et al (2004) in general for biological ice nuclei.

These possible interactions with the weather and climate system as well as the fact that fungi are one of the major contributors of bioaerosols makes it crucial to gain more knowledge about the circumstances and amounts in which they are emitted and about their transport behaviour. Recently there have been various modelling studies on potential impacts from biological aerosols on clouds, which have reached different conclusions (Möhler et al 2008, Phillips et al 2008, Burrows et al 2009, Hoose et al 2010, Sesartic et al 2012). While Hoose et al (2010) do not find any significant impact of bioaerosols on clouds and precipitation, e.g. Phillips et al (2008) state that cloud properties are altered by boosted bacterial concentrations. Sesartic et al (2012) find that bacteria contribute to total freezing more strongly than dust, but the reason that only small changes in cloud properties are visible is because bacteria are less numerous and they largely replace dust particles acting as ice nuclei. The studies agree that there is no impact to be observed with realistic bioaerosol concentrations. However, it needs to be noted that sampling of fungal spores and other bioaerosols lacked a standardized procedure so far, which may lead to vast uncertainties and very different observed bioaerosol concentrations which are used as input in the global climate models.

In the present study we aim to examine the influence of fungal spores on microphysical properties of stratiform clouds and precipitation on a global scale, using observational data compiled by Sesartic and Dallafior (2011) in order to get a first estimate of the possible impacts. In section 2, the global climate model and experimental design are described. Results from sensitivity tests are shown and discussed in section 3.

2. Model setup

ECHAM5 is the fifth generation atmospheric general circulation model (GCM) that evolved from the model of the European Centre for Medium Range Weather Forecasting (ECMWF) and was further developed at the Max-Planck Institute for Meteorology (Roeckner et al 2003). The model solves prognostic equations for vorticity, divergence, temperature and surface pressure using spherical harmonics with triangular truncation. Water vapour, cloud liquid water and ice, as well as trace components, are transported using a semi-Lagrangian scheme (Lin and Rood 1996) on a Gaussian grid. Prognostic equations for cloud water and ice follow Lohmann et al (2007). The model includes the cirrus scheme of Kärcher and Lohmann (2002). Convective clouds and transport are based on the mass-flux scheme of Tiedtke (1989) with modifications following Nordeng (1994). The solar radiation scheme has 6 spectral bands (Cagnazzo et al 2007) and the infrared has 16 spectral bands (Mlawer et al 1997, Morcrette et al 1998).

The GCM is coupled to the Hamburg Aerosol Model (HAM), which is described in detail by Stier et al (2005) and most recently adapted by Lohmann and Hoos (2009). The aerosols are represented by seven log-normal modes, four internally mixed/soluble modes (nucleation (NS), Aitken (KS), accumulation (AS), and coarse (CS)) and three insoluble modes (Aitken (KI), accumulation (AI), and coarse (CI)). The median radius for each mode is calculated from the aerosol mass and number distributions in each mode. Aerosol mass and number are transferred between the modes by the processes of sulfuric acid condensation, and coagulation between aerosols.

Fungal spores were introduced as a new aerosol species into HAM which was recently augmented by Sesartic et al (2012) to include bioaerosol modes (see table 1). Fungal spores are emitted initially in the bioaerosol insoluble mode. They can be transferred to the mixed mode by coating with $H_2SO_4$ and coagulation with sulfate, black carbon and organic carbon. It is assumed that fungal spores behave similarly to bacteria, and are thus allowed to coagulate with dust, as this process has been observed for bacteria in nature (Griffin 2007). According to Pouleur et al (1992), the freezing behaviour of IN active fungal spores is comparable to that of the bacterium Pseudomonas sp. Therefore the same parameterizations for contact freezing of fungal spores as those for bacteria from Diehl et al (2006), and analogous for the immersion freezing Diehl and Wurzler (2004) are used. The limitation of this assumption is that Pouleur et al (1992) only reported $F.\ avenaceum$ spores to have similar freezing behaviours like bacteria (freezing behaviour of other fungal spore types is still rather uncertain). Deposition nucleation on fungal spores is not considered, because the observational data are missing. As there are no data available about shortwave and longwave radiative properties of fungal spores, but they have a similar refractive index as sea salt (Ebert et al 2002) the identical data as for sea salt (Fenn et al 1981) were assumed for fungal spore shortwave and longwave radiative properties.
with F from the JSBACH dynamic vegetation model (Raddatz et al.) functional type and the seasonally changing leaf area index. These effects are taken into account by obtaining the plant emissions of fungal spores differ for different plant functional types and they change with season.

Spracklen (2009). The emissions of fungal spores differ for different plant functional types and they change with season. These effects are taken into account by obtaining the plant functional type and the seasonally changing leaf area index from the JSBACH dynamic vegetation model (Raddatz et al. 2007). These data are combined with observed near surface fungal spore fluxes (Sesartic and Dallafior 2011) and used as an input for ECHAM5.

The emission flux \( F \) of fungal spores is calculated in ECHAM5 analogue to Sesartic et al. (2012)

\[
F = \sum_{i=5}^{5} f_i F_i
\]

with \( F_i \) being the fungal spore number emission flux \((\text{m}^{-2} \text{ s}^{-1})\) over a particular ecosystem, \( f_i \) denoting the fractional coverage of a gridbox with a certain ecosystem, and \( i \) standing for crops, grass, shrubs, forests and land ice. Due to the limited available data on emissions of fungal spores in the air, the ecosystem types available in JSBACH which are acting as IN are detailed in Stier et al. (2005).

The natural emissions of sea salt, dust, and dimethyl sulfate (DMS) from the oceans are calculated on-line, based on the meteorology of the model. Emissions for all other aerosol species are taken from the AEROCOM emission inventory, and are representative for the year 2000 (Dentener et al. 2006). The aerosol emissions and the removal processes of in cloud scavenging, sedimentation, and dry deposition are described in detail in Stier et al. (2005).

### Table 2. Simulations.

| Simulation | Description |
|------------|-------------|
| CTL        | Control simulation. No bioaerosols acting as IN |
| FNG1       | Fungal spores best-estimate emissions (Sesartic and Dallafior 2011) |
|            | 1% of fungal spores IN active |
| FNG10      | Fungal spores best-estimate emissions (Sesartic and Dallafior 2011) |
|            | 10% of fungal spores IN active |
| FNG100     | Fungal spores best-estimate emissions (Sesartic and Dallafior 2011) |
|            | 100% of fungal spores IN active |
| BT1FNG1    | Bacteria best-estimate emissions (Burrows et al. 2009) |
|            | 1% of bacteria IN active |
|            | Fungal spores best-estimate emissions (Sesartic and Dallafior 2011) |
|            | 1% of fungal spores IN active |

All results presented in this study are from simulations which have been integrated for one year, following a three months spin-up period. All simulations are nudged to the ECMWF ERA40 reanalysis data for the year 2000 (Simmons and Gibson 2000), according to the nudging technique described by Timmreck and Schulz (2004). The spectral resolution of all simulations is T42 which corresponds to 2.8125° × 2.8125° horizontally, with 19 vertical levels from the surface up to 10 hPa and a 30 min time step.

All simulations conducted in this study are summarized in table 2. In the reference simulation (CTL) bioaerosols act only as passive tracer, i.e. fungal spores are emitted and transported around the globe, but have no effects on the radiation budget, cloud microphysics and precipitation. In all the other simulations (cf table 1) the bioaerosol are allowed to act as IN. In the simulations FNG1, FNG10 and FNG100 fungal spore best-estimate emissions from Sesartic and Dallafior (2011) are used and the fraction of fungal spores acting as IN is varied from 1% to 10% and 100%, respectively. The simulation BT1FNG1 includes bacteria best-estimate emissions from Burrows et al. (2009) and fungal spore best-estimate emissions from Sesartic and Dallafior (2011) with 1% of both bacteria and fungal spores acting as IN.

### Table 3. Global fungal spore emissions and burdens calculated with ECHAM5-HAM compared to the model results by Winiwarter et al. (2009) and Jacobson and Streets (2009).

| Emissions \((\text{Tg yr}^{-1})\) | Burden \((\text{Tg})\) | Source |
|---------------------------------|----------------|--------|
| 3.972                           | 0.001          | ECHAM5 best-estimate fungal spore emissions |
| 50                              | n/a            | Elbert et al. (2007) |
| 28                              | 0.018          | Heald and Spracklen (2009) |
| 31                              | 0.094          | Hoose et al. (2010) |
| 186                             | n/a            | Jacobson and Streets (2009) |
| 0.23                            | n/a            | Winiwarter et al. (2009) |

3. Results and discussion

The annual zonal mean vertical profiles of dust, bacteria and fungal spore number concentrations, as depicted in figure 1 show that there is transport of bacteria to the middle and upper troposphere. However, their number concentrations in the troposphere are two to three orders of magnitude lower than that for dust, and the number of fungal spores is in turn two to three orders of magnitude lower than those for bacteria. This is not surprising as fungal spores are larger than bacteria.

Compared to the fungal spore emissions and burdens calculated by Elbert et al. (2007), Heald and Spracklen (2009), Jacobson and Streets (2009) and Hoose et al. (2010), ECHAM exhibits emissions an order of magnitude smaller, and shows the smallest burden of all models apart from Winiwarter et al. (2009) (see table 3). This means that fungal spores are efficiently washed out of the atmosphere, due to their relatively large mass for an aerosol. It is interesting to note that the ratio of emission to burden is fairly similar to that of
Heald and Spracklen (2009), while Hoose et al (2010) seem to have a much slower removal.

The results from the BT1FNG1 simulation in figure 2 show the emission, deposition and burden of fungal spores as compared to bacteria. It is evident from the figure that fungal spores behave similar to bacteria. They are equally transported over large distances and their deposition is enhanced over areas with lots of vegetation and high amounts of precipitation, e.g. the Amazon, the Congo basin, or South-East Asia. However, as fungal spores are rather large, they also show relatively large mass burdens and large mass emission, despite their smaller number emission compared to bacteria.

Unfortunately, to the best of our knowledge, there is no observational data on the dry and wet deposition of fungal spores available, thus allowing only for a relative comparison of fungal spores to bacteria.

However, fungal spore observations over the Atlantic and North America conducted by sampling from aircraft at three different altitudes, allowed for a comparison of the observed vertical fungal spore number concentration with ECHAM5-HAM (Fulton and Mitchell 1996, Fulton 1996a, 1996b, 1996c) (see table 4). In order to compare the model values with observations, the model values were interpolated to the location of the measurements and multiplied by a factor of 0.8 in order to account for about 80% of the total fungal spores being viable (Adhikari et al 2004). Judging by the available data, the model appears to underestimate the availability of fungal spores at altitudes relevant for low to mid-level cloud formation.

According to Gregory (1962) only 10% of fungal spores belong the escape fraction (i.e. are transported further than 100 m) from their emission source. In turn, we assumed 10% of those spores to belong to an IN active species. Therefore, only 1% of fungal spores is said to act as active IN in the end. This is realized in the FNG1 simulation, that we assume to be the best estimate. In this simulation we see a slight reduction in liquid water content (LWC) and increase in ice water content (IWC), which is expected, as bioaerosols (bacteria and fungal spores) were shown to be efficient IN (Morris et al 2011). The IWC is slightly higher in the heterogeneous freezing regime, while the LWC is lower. Between 30 and 60°N our simulation indicates a reduction in the ice crystal number concentration (ICNC), which can be explained by the increase in the effective radius of ice crystals (see figure 3). As fungal spores are large IN, the resulting ice crystals are larger in FNG1 than in CTL. Also, since they are more efficient IN than dust, fungal spores form a few ice crystals first and can in some cases deplete liquid water by growing via the Wegener–Bergeron–Findeisen process and thus leaving less water available for other potential ice nuclei like mineral dust. This gives us fewer but larger ice crystals, thus explaining the decrease in ICNC and the parallel slightly increased IWC. The changes in IWC are most pronounced in the Arctic due to the fact that temperatures there are in the range of mixed-phase clouds (0 to −35 °C) for large parts of the year even at the surface, so the fungal spores do not have to be transported high up into the atmosphere to have an impact in this region. Around the Arctic circle there are vast areas of tundra and boreal forests which are providing fungal spore sources for the Arctic. This is also evident in the zonal mean fungal spore concentration in figure 1.

The changes for the liquid water path (LWP), ice water path (IWP), cloud droplet number concentration (CDNC), ice crystal number concentration (ICNC), precipitation, cloud cover, relative humidity, shortwave (SCF) and longwave cloud forcing (LCF), as well as the aerosol optical depth (AOD) in the simulations with fungal spores as compared to the reference simulation remain small (cf table 5). Generally, the CDNC slightly decreases and ICNC increases as compared to the reference simulation. As expected, the IWP increases while the LWP decreases due to the earlier onset of the Bergeron–Findeisen process if fungal spores as additional IN are available. The changes in LWP and IWP are very small but

| Altitude (m a.s.l.) | Observations (m$^{-3}$) | FNG1 (m$^{-3}$) |
|--------------------|-------------------------|----------------|
| 915                | 125                     | 5.03           |
| 1825               | 24.2                    | 3.43           |
| 3332               | 8.70                    | 0.20           |

# Table 4. Global fungal spore number concentrations annual mean from observations (Fulton and Mitchell 1996, Fulton 1996a, 1996b, 1996c) and the FNG1 model simulation for three altitudes.

Figure 1. Modelled (CTL) annual zonal mean vertical profiles of dust, bacteria and fungal spore mass and number concentrations (cm$^{-3}$).
a consistent feature throughout the simulations. The largest changes in the cloud droplet and ice crystal concentration are observed when all fungal spores act as IN (simulation FNG100).

In figure 4 an increase in stratiform precipitation and snowfall can be seen both in FNG1 and FNG100 simulations. As the Arctic cloud cover is mainly dominated by semi-permanent low-level clouds (Zygmuntowska et al 2012), the fungal spores would not need to ascend high in order to have an effect on mixed-phase clouds in this region. Additionally, the continents of North America and Asia with their vast expanse of tundra and boreal forests would act as sources of fungal spores.

Finally, if SCF and LCF are combined into a total cloud radiative forcing, a slight warming effect can be observed for all simulations. While on a global scale it might not be as strong, it can still have an important impact in vulnerable regions like the Arctic. However, if one were to look at the FNG100 simulation, on a global average fungal spores would lead to a shortwave warming by $0.32 \text{ W m}^{-2}$ simulation. This warming is partly compensated by longwave cooling of $0.10 \text{ W m}^{-2}$, but the net is still a warming of $0.22 \text{ W m}^{-2}$. Given that our simulated concentrations are on the low side compared to other studies and observations, we think it evident that a further research into climate effects of fungal spores and other bioaerosols is necessary.
Figure 3. Modelled annual zonal mean weighted effective ice crystal radius (µm) for CTL and the difference between FNG1, FNG10 and FNG10 regarding CTL.

Table 5. Yearly average values for the simulations CTL, FNG1, FNG10, FNG100 and BT1FNG1 compared to observations (OBS). The table displays LWP, IWP, total cloud cover (TCC), CDNC, ICNC, total precipitation (P), SCF, LCF, radiation budget at the top of the atmosphere $F_{net}$ and the AOD. See table 2 for the description of the simulation acronyms. Global averaged annual estimates and zonal mean estimated observational data are taken from the Global Precipitation Climatology Project (GPCP) for total precipitation $P_{tot}$ (Huffman et al, 1997, Adler et al 2003). LWP stem from satellite (SSM/I) retrievals by Wentz (1997), Greenwald et al (1993) and Weng and Grody (1994). IWP is derived from ISCCP data (Storelvmo et al, 2008). Cloud droplet number concentration $N_l$ retrievals from Han et al (1998) is available for 50°N to 50°S SCF and LCF are deduced from Kiehl and Trenberth (1997). AOD are provided by Schulz et al (2006) and Kinne (2008). TCC observations are derived from observations of ISCCP (Rossow and Schiffer, 1999), surface observations collected by Hahn et al (1995) and satellite observations estimated by Stubenrauch and Kinne (2009).

| ECHAM5.5- | CTL | FNG1 | FNG10 | FNG100 | BT1FNG1 | OBS |
|-----------|-----|------|-------|--------|---------|-----|
| LWP (g m⁻²) | 56.64 | 56.09 | 55.78 | 55.22 | 56.14 | 48–83 |
| IWP (g m⁻²) | 6.965 | 6.973 | 6.991 | 7.016 | 6.974 | 29 |
| TCC (%) | 60.12 | 59.94 | 59.98 | 59.97 | 60.00 | 65–75 |
| $N_l$ (10¹⁰ m⁻²) | 3.418 | 3.376 | 3.372 | 3.371 | 3.379 | 4 |
| $N_i$ (10¹⁰ m⁻²) | 0.124 | 0.125 | 0.120 | 0.117 | 0.121 | — |
| P (mm d⁻¹) | 2.839 | 2.842 | 2.842 | 2.842 | 2.842 | 2.74 |
| SCF (W m⁻²) | −48.81 | −48.60 | −48.59 | −48.49 | −48.69 | −47 to −50 |
| LCF (W m⁻²) | 26.32 | 26.29 | 26.29 | 26.22 | 26.31 | 2–30 |
| AOD | 0.117 | 0.125 | 0.125 | 0.125 | 0.125 | 0.15–0.18 |
4. Conclusions

Fungal spores as a new aerosol particle species were introduced into ECHAM5-HAM. The model captures the observed fungal spore emissions satisfactorily. The inclusion of fungal spores acting as ice nuclei in a GCM leads to negligible changes in cloud formation and precipitation on a global level. Nevertheless, changes in the liquid water path and ice water path can be observed, specifically in the boreal regions where tundra and forests act as sources of fungal spores. This goes hand in hand with a decreased ICNC and increased effective radius of ice crystals. An increase in stratiform precipitation and snowfall can be observed in those regions as well. These results for fungal spores are comparable to the ones achieved with bacteria (Sesartic et al 2012). More observational data about fungal spore emissions and deposition, as well as in situ measurements inside clouds and vertical profiles are needed for a better comparison of model results with the observations. There are currently several uncertainties constraining the modelling of the impact of fungal spores on climate and precipitation, for example their exact emissions, size distributions, ice nucleation active fractions etc. Further research should focus on regional and local effects of fungal spores, especially in the tropical and boreal regions where a potential impact on local climate might be expected.

Acknowledgment

The authors are grateful to Sylvaine Ferrachat for her technical support with ECHAM5.

References

Adhikari A et al 2004 Sci. Total Environ. 326 123–41
Adler R et al 2003 J. Hydrometeorol. 4 1147–67
Baron P and Willeke K 2001 Aerosol Measurement—Principles, Techniques and Applications 2nd edn (Toronto: Wiley)
Burgess H A 2002 J. Allergy Clin. Immunol. 110 544–52
Burrows S et al 2009 Atmos. Chem. Phys. 9 9281–97
Cagnazzo C et al 2007 Atmos. Chem. Phys. 7 2503–15
Dentener F et al 2006 Atmos. Chem. Phys. 6 4321–44
Diehl K et al 2006 J. Geophys. Res.—Atmos. 111 D07202
Diehl K and Wurzler S 2004 J. Atmos. Sci. 61 2063–72
Ebert M et al 2002 J. Geophys. Res.—Atmos. 107 8121
Elbert W et al 2007 Atmos. Chem. Phys. 7 4569–88
Fenn R W et al 1981 Atmos. Environ. 15 1911–8
Fulton J D 1996a Appl. Microbiol. 14 237ff
Fulton J D 1996b Appl. Microbiol. 14 241ff
Fulton J D 1996c Appl. Microbiol. 14 245ff
Fulton J D and Mitchell R B 1996 Appl. Microbiol. 14 232ff
Greenwald T J et al 1993 J. Geophys. Res. 98 18471–88
Gregory P H 1962 Pollen Spores 348
Gregory P H 1967 Sci. Prog. 55 613–28
Griffin D W 2001 Aerobiologia 3 203–13
Griffin D W 2006 Aerobiologia 22 211–26
Griffin D W 2007 Clin. Microbiol. Rev. 20 459–77
Hahn C et al 2003 J. Clin. Immunol. 18 1429–46
Han Q et al 1998 Geophys. Res. Lett. 25 1419–22
Heald C L and Spracklen D V 2009 Geophys. Res. Lett. 36 L09806
Hoose C et al 2010 Environ. Res. Lett. 5 024009
Huffman G et al 1997 Bull. Am. Meteorol. Soc. 78 5–20
Huffman G et al 1998 Bull. Am. Meteorol. Soc. 79 399–401
Huffman J A et al 2012 Atmos. Chem. Phys. 12 11997–2019
Huffman J A et al 2013 Atmos. Chem. Phys. Discus. 13 11767–93
Jannone R et al 2011 Atmos. Chem. Phys. 11 1191–201
Johansen M and Streets D G 2009 J. Geophys. Res.—Atmos. 114 D08118
Jaenicke R et al 2007 Environ. Chem. 4 217
Kärcher B and Lohmann U 2002 J. Geophys. Res. 107 AAC 4–1–10
Kieft T L 1988 Appl. Environ. Microbiol. 54 1678–81
Kieft T L and Rustegi T 1990 J. Bacteriol. 172 3519–23
Kiehl J T and Trenberth K E 1997 Bull. Am. Meteorol. Soc. 78 197–208
Kinne S 2008 personal communication
Lin S and Rood R 1996 Mon. Weather Rev. 124 2046–70
Lohmann U and Hoose C 2009 Atmos. Chem. Phys. 9 8917–34
Lohmann U et al 2007 Atmos. Chem. Phys. 7 3425–46
Mlawer E et al 1997 J. Geophys. Res.—Atmos. 102 16663–82
Möhler O et al 2008 Biogeosciences 5 1425–35
Morcrette J et al 1998 Impact of a Validated Radiative Transfer Scheme, RRTM, on the ECMWF Model Climate and 10-day Forecasts (Reading, MA: ECMWF)
Morris C et al 2004 J. Physique IV 121 87–103
Morris C et al 2011 Biogeosciences 8 17–25
Nordeng T E 1994 Extended Versions of the Convective Parameterization Scheme by ECMWF and their Impact on the Mean and Transient Activity of the Model in the Tropics (Reading, MA: ECMWF)
Olson J S 1992 Digital raster data on a 10 min Cartesian orthonormal geodetic 1080 × 2160 grid Global Ecosystems Database, Version 2.0 (Boulder, CO: National Geophysical Data Center)
Phillips V T J et al 2008 Biogeosciences 6 987–1014
Poulter S et al 1992 Appl. Environ. Microbiol. 58 2960–4
Pratt K et al 2009 Nature Geosci. 2 397–400
Prenni A J et al 2009 Nature Geosci. 2 401–4
Prospero J et al 2005 Aerobiologia 21 1–19
Raddatz T J et al 2007 Clim. Dyn. 29 565–74
Roeckner E et al 2003 The atmospheric general circulation model ECHAM5. Part I: model description Technical Report 349 (Hamburg: Max Planck Institute for Meteorology)
Rossow W B and Schiffer R A 1999 Bull. Am. Meteorol. Soc. 80 2261–87
Schulz M et al 2006 Atmos. Chem. Phys. 6 5225–46
Seinfeld J H and Pandis S 2006 Atmospheric Chemistry and Physics: From Air Pollution to Climate Change 2nd edn (New York: Wiley)
Sesartic A and Dallaiñor T N 2011 Biogeosciences 8 1181–92
Sesartic A et al 2012 Atmos. Chem. Phys. 12 8645–61
Simmons A J and Gibson J K 2000 The ERA-40 Project Plan (Reading, MA: ECMWF)
Stier P et al 2005 Atmos. Chem. Phys. 5 1125–56
Storelvmo T et al 2008 J. Atmos. Sci. 65 3214–30
Stubenrauch C, Kinne S and GEWEX Cloud Assessment Team 2009 Evaluation of global cloud data products GEWEX News 19 (1) 6–7
Tiedtke M 1989 Mon. Weather Rev. 117 1779–800
Timmreck C and Schulz M 2004 J. Geophys. Res. 109 D13202
Weng F and Grody N C 1994 J. Geophys. Res. 99 25535–51
Wenjen P J 1997 J. Geophys. Res. 102 8703–18
Winiger W, Bauer H, Caseiro A and Puxbaum H 2009 Atmos. Environ. 43 1403–9
Zygmuntowska M, Mauritsen T, Quaas J and Kaleschke L 2012 Atmos. Chem. Phys. 12 6667–77