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

2013 Environ. Res. Lett. 8 014029

(http://iopscience.iop.org/1748-9326/8/1/014029)

OPEN ACCESS
IOP PUBLISHING
ENVIRONMENTAL RESEARCH LETTERS
Environ. Res. Lett. **8** (2013) 014029 (8pp)
doi:10.1088/1748-9326/8/1/014029

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

Ana Sesartic[1], Ulrike Lohmann[1] and Trude Storelvmo[2]

[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

Table 1. The modal structure of HAM with its aerosol species: sulfate (SO_4), black carbon (BC), organic carbon (OC), sea salt (SS), mineral dust (DU), bacteria (BCT) and fungal spores (FNG). The radius range of the aerosol particles in the respective mode is given by r. 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 r	Size range (μm)	Mixed/soluble	Insoluble
Nucleation	$r \leq 0.005$	SO_4	—
Aitken	$0.005 < r \leq 0.05$	SO_4, BC, OC	BC, OC
Accumulation	$0.05 < r \leq 0.5$	SO_4, BC, OC, SS, DU	DU
Coarse	$0.5 < r \leq 1$	SO_4, BC, OC, SS, DU	DU
Bioaerosol	$1 < r$	SO_4, 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 Hoose (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.

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

The standard deviation of the fungal spore distribution was set to 2, equal to that of bacteria. The mean mass scavenging coefficient for fungal spores scavenged by rain was set to 1 and to 5×10^{-3} kg m^{-2} for fungal spores scavenged by snow, as estimated from Seinfeld and Pandis (2006). The average mass of a fungal spore in ECHAM is assumed to be 33×10^{-15} kg and its average density was calculated as being 0.85 g cm^{-3} from data available in Baron and Willeke (2001).

The primary source of fungal aerosols are plants (Burgess 2002), soil, litter and decaying organic matter (Heald and 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)

$$F = \sum_{i=5}^{5} f_i F_i \quad (1)$$

with F_i being the fungal spore number emission flux (m^{-2} 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 based on the Olson World Ecosystems dataset (Olson 1992) were lumped into the aforementioned five groups.

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 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 (Tg yr^{-1})	Burden (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)

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.

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

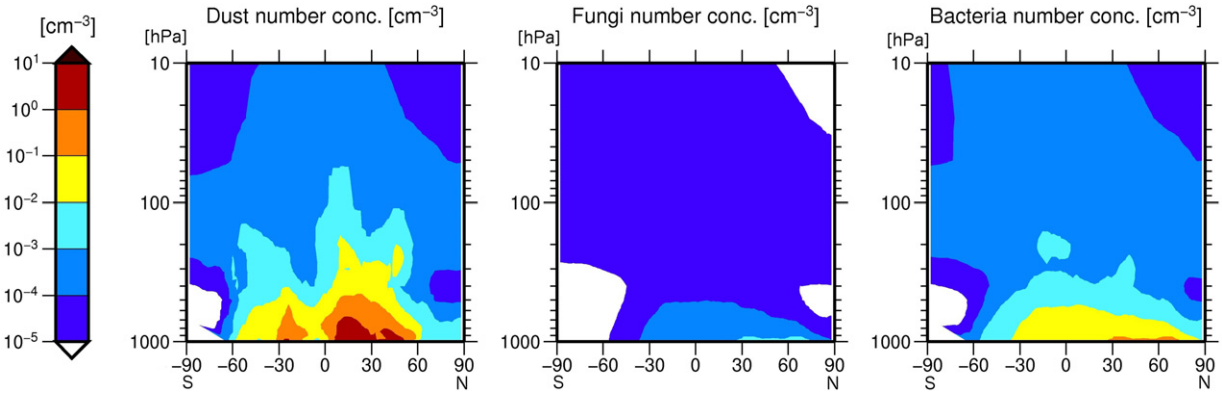

Figure 1. Modelled (CTL) annual zonal mean vertical profiles of dust, bacteria and fungal spore mass and number concentrations (cm^{-3}).

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.

Altitude (m a.s.l.)	Observations (m^{-3})	FNG1 (m^{-3})
915	125	5.03
1825	24.2	3.43
3352	8.70	0.20

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

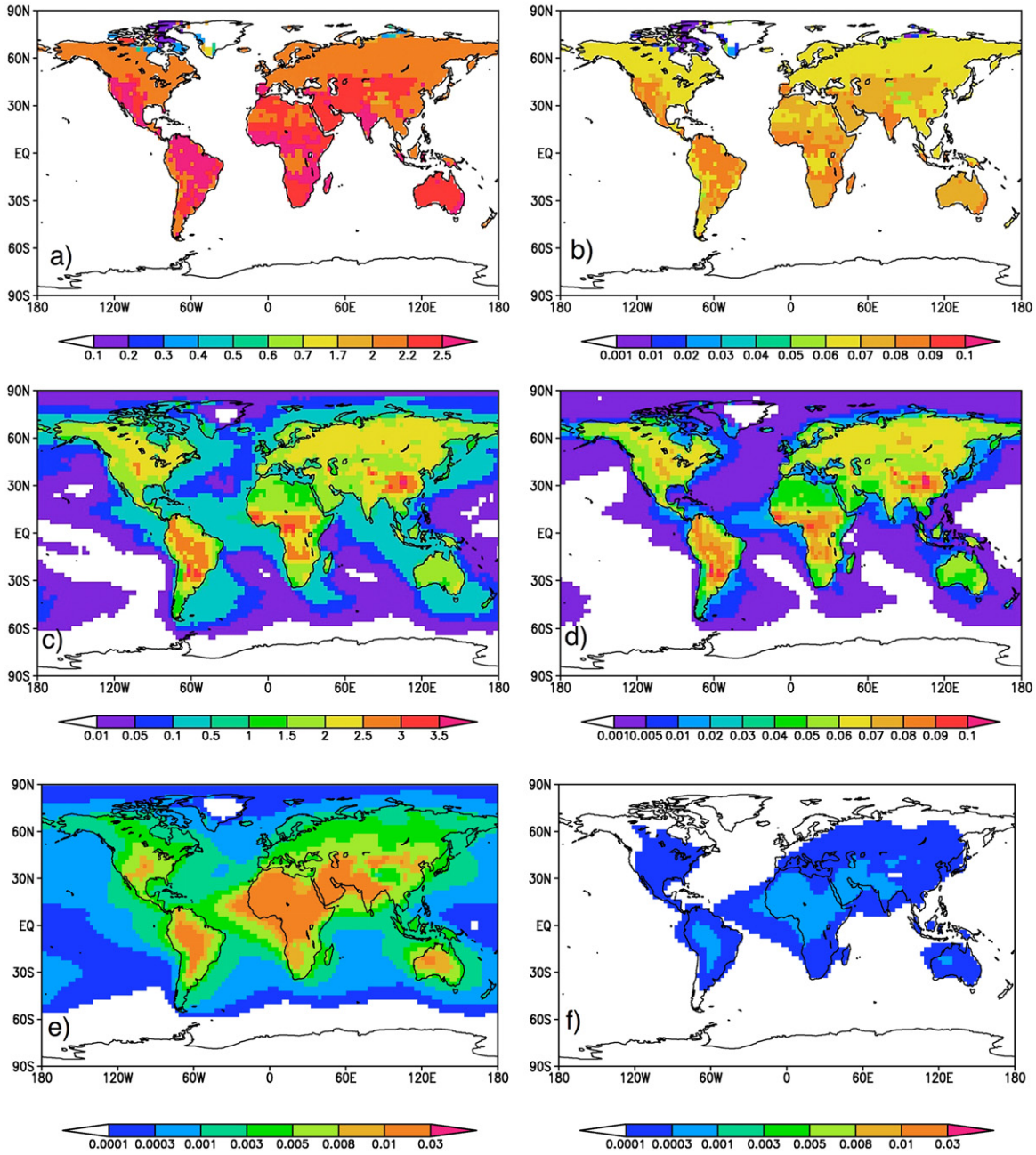

Figure 2. Modelled (BT1FNG1, see table 2 for description) annual means of emission, deposition and burden of fungal spores and bacteria. (a) Fungal spore emission (g m^{-2} yr^{-1}), (b) bacteria emission (g m^{-2} yr^{-1}), (c) fungal spore deposition (g m^{-2} yr^{-1}), (d) bacteria deposition (g m^{-2} yr^{-1}), (e) fungal spore burden (g m^{-2}), (f) bacteria burden (g m^{-2}).

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 W m^{-2} simulation. This warming is partly compensated by longwave cooling of 0.10 W m^{-2}, but the net is still a warming of 0.22 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.

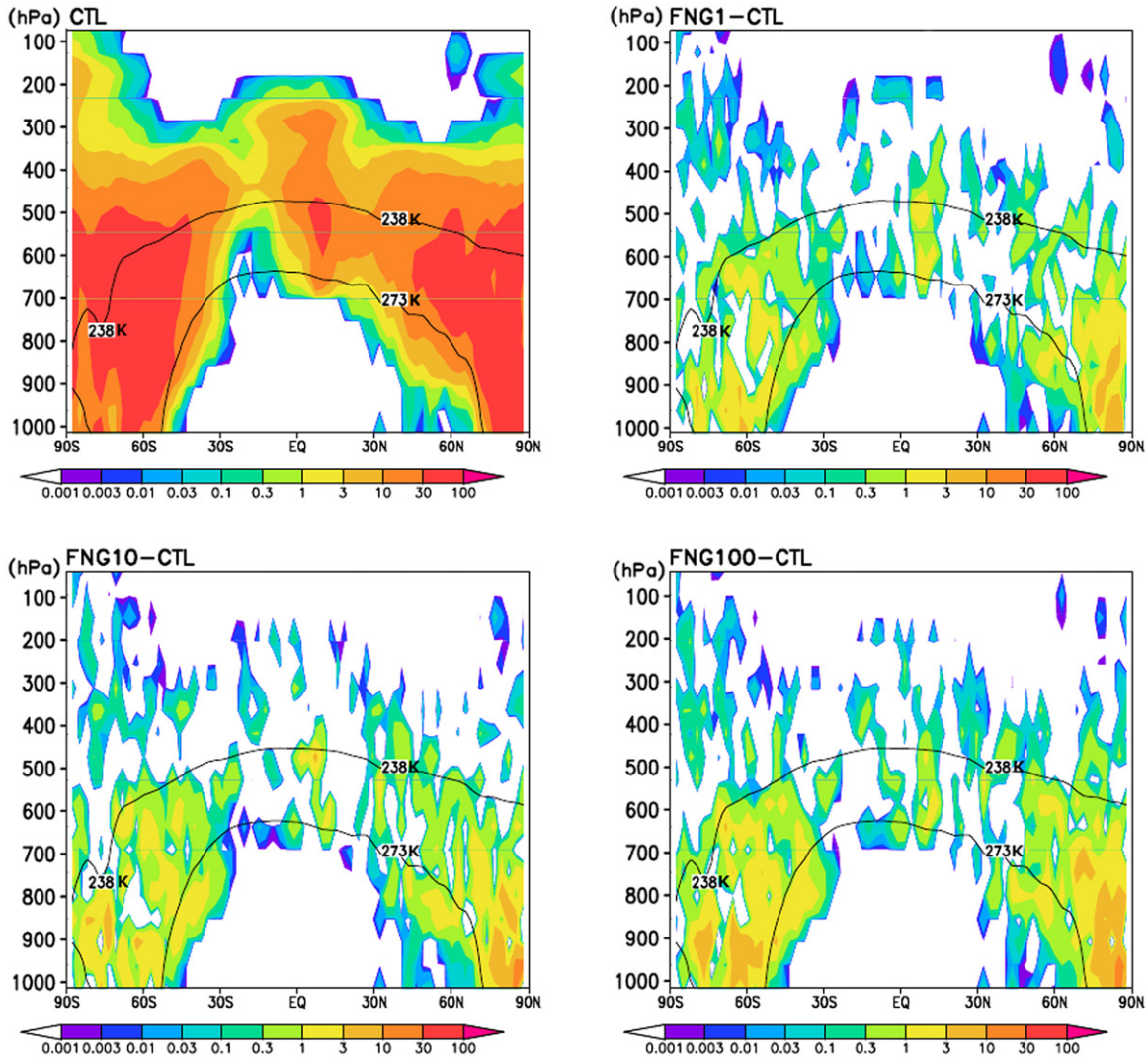

Figure 3. Modelled annual zonal mean weighted effective ice crystal radius (μm) for CTL and the difference between FNG1, FNG10 and FNG10 regarding CTL.

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 (10^{10} m^{-2})	3.418	3.376	3.372	3.371	3.379	4
N_i (10^{10} 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

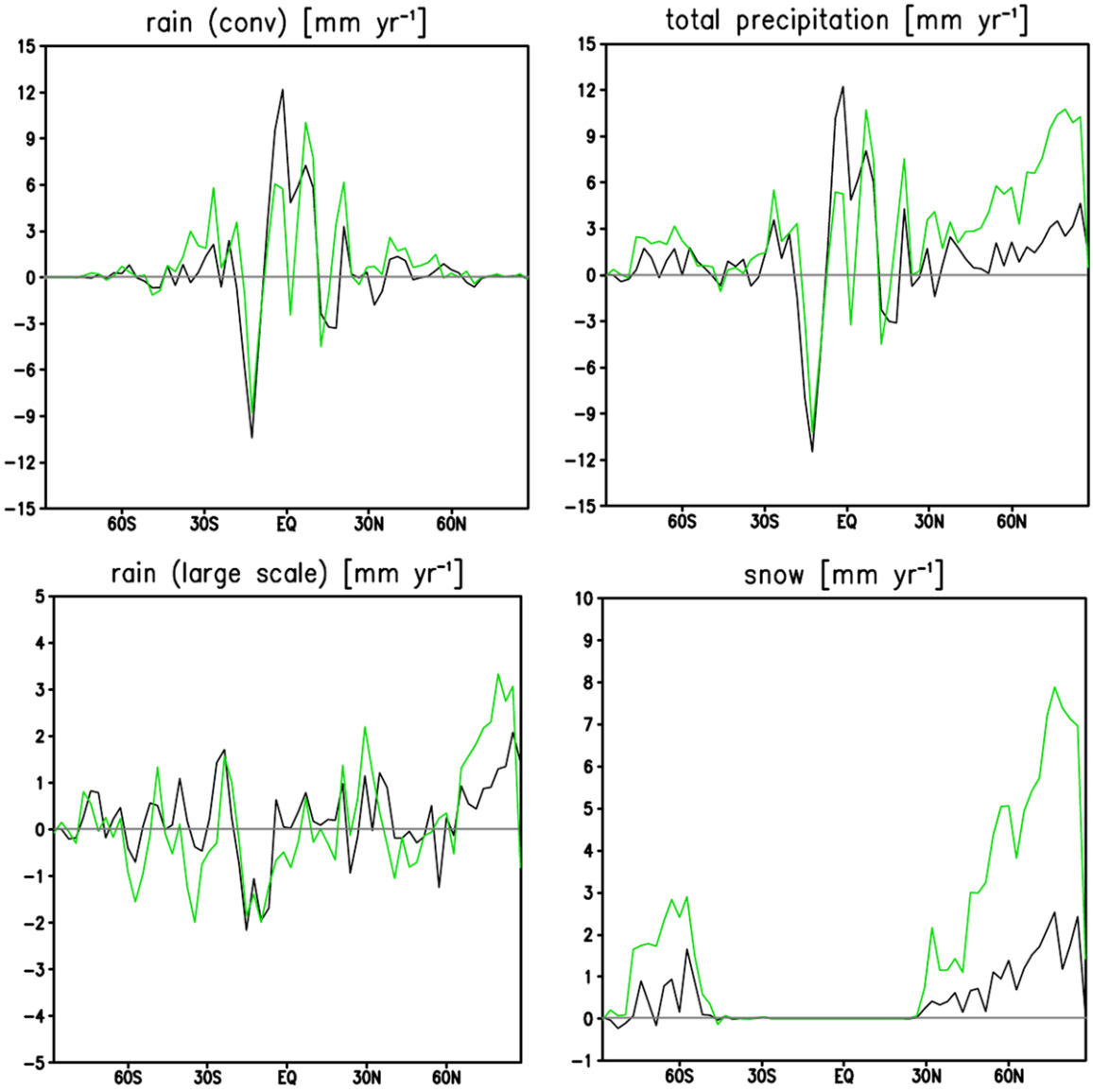

Figure 4. Modelled annual zonal mean differences in precipitation between CTL and FNG1 (black), and CTL and FNG100 (green) simulations.

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* 1995 *J. Clim.* **8** 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 J A *et al* 2012 *Atmos. Chem. Phys.* **12** 11997–2019
Huffman J A *et al* 2013 *Atmos. Chem. Phys. Discuss.* **13** 1767–93
Iannone R *et al* 2011 *Atmos. Chem. Phys.* **11** 1191–201
Jacobson 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 Ruscetti 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
Pouleur 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 Dallafior 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
Wentz F J 1997 *J. Geophys. Res.* **102** 8703–18
Winiwarter 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