

Global fungal spore emissions, review and synthesis of literature data

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Global fungal spore emissions, review and synthesis of literature data

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Abstract

The present paper summarizes fungal spore emission fluxes in different biomes. A literature study of more than 150 papers has been conducted and emission fluxes have been calculated based on 35 fungal spore concentration datasets. Biome area data has been derived from the World Resource Institute. Several assumptions and simplifications needed to be adopted while aggregating the data: results from different measurement methods have been treated equally, while diurnal and seasonal cycles have been neglected. Moreover flux data were aggregated to very coarse biome areas due to scarcity of data. Results show number fluxes per square meter and second of 3.13 for forest, 24.7 for shrub, 31.77 for crop, 0.03 for tundra, and 1.45 for grassland. No data were found for land ice. The annual mean global fluxes amount to $4 \times 10^{-13} \text{ kgm}^{-2} \text{ s}^{-1}$ as the best estimates, and $2.2 \times 10^{-13} \text{ kgm}^{-2} \text{ s}^{-1}$ and $8.9 \times 10^{-13} \text{ kgm}^{-2} \text{ s}^{-1}$ as the low and high estimate, respectively.

1 Introduction

Fungal spores are part of the bioaerosol population in our atmosphere which also comprises components such as pollen, bacteria or viruses. Interest in bioaerosols is mainly related to their health effects, agriculture, ice nucleation and cloud droplet activation or atmospheric chemistry (Ariya et al., 2009). In the present study, the focus lies on fungal aerosols.

Measurements of fungal aerosols report average ground level concentrations of around 10 000–50 000 spores m^{-3} , sometimes even exceeding 200 000 spores m^{-3} (Levetin, 1995). This is two orders of magnitude higher than observed peak pollen concentrations (1000–2000 grains m^{-3}) (Mandrioli, 1998). Froehlich-Nowoisky et al. (2009) also state that up to 45% of the coarse particle mass in tropical rainforest air consists of fungal spores. Jaenicke et al. (2007) found that fungal spores are the main contributor to the bioaerosol mass in the Amazon basin. Simulations conducted by

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Heald and Spracklen (2009) came to the conclusion that 23% of all primary emissions of organic aerosol are of fungal origin. Investigations of Bauer et al. (2002b) have shown that “5.8% of the organic carbon in the coarse aerosol mode” was due to fungal spores and bacteria. When sampling bioaerosols at the Rothampsted Experimental Station in the south of England, Gregory (1978) found that they mainly consisted of fungal spores; nearly half of a fair weather sample consisted of *Cladosporium* spores (a mould) and only one percent of all bioaerosols were plant pollen. These findings show that fungal spores are an non-negligible part of the atmospheric aerosol.

The primary source of fungal aerosols are plants (Burgess, 2002), soil, litter and decaying organic matter (Heald and Spracklen, 2009). Release mechanisms of fungal spores are numerous and vary from species to species (Elbert et al., 2007; Gregory, 1967, 1973; Levetin, 1995; Jones and Harrison, 2003; Madelin, 1994; Hirst, 1953). Generally, release of spores is highly dependent on meteorological factors. Some require rather humid conditions whereas others favour dry and windy conditions for spore release. Several studies have been conducted on the relationship between meteorological factors and spore concentrations. Significant correlations between spore counts and wind speeds could be found (Glikson et al., 1995) as well as a positive correlation of *Alternaria* spore counts with temperature (Burch and Levetin, 2002). Stepalska and Wolek (2009) on the other hand could not find a significant correlation of spore concentrations with weather conditions for most species investigated in their study. It is hence difficult to predict which and how many spores are released according to weather conditions.

As for their transport behaviour, most of the spores do not travel very long distances. As calculations by Gregory (1962) have shown only a fraction of about 10% of all released fungal spores is transported farther away than 100m. This fraction is called the “escape fraction”. Wind speed, temperature, atmospheric pressure or precipitation are important conditions determining transport and deposition of the dispersed aerosols (Hirst et al., 1967). There is evidence that fungal spores can also be transported over long distances (Griffin et al., 2006, 2001; Prospero et al., 2005) before

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they are deposited either due to gravity, wash-out by rain or impactation (Gregory, 1967). Among others, Prospero et al. (2005) found fungal spores originating from the African desert to influence the prevailing fungal spore concentrations on the Virgin Islands in the Caribbean.

5 Some fungal spores can act as very effective ice nucleators. Lichen were found to nucleate ice at temperatures higher than -8°C and some even at temperatures higher than -5°C (Kieft, 1988). The lichen fungus *Rhizoplaca chrysoleuca* was even found to be an active ice nucleus at temperatures as high as -2°C (Kieft, 1988; Kieft and Ruscetti, 1990). To date, only a few fungus species have been found to be active
10 ice nucleators: besides the above mentioned lichen these are *Fusarium avenaceum* and *Fusarium acuminatum* (Pouleur et al., 1992). The ice nucleating activity of *F. avenaceum* is comparable to that of the bacterium *Pseudomonas* sp. (Pouleur et al., 1992). In contrast to those findings is the recent research by Iannone et al. (2010) that showed poor ice nucleation ability of *Cladosporium* spores, with immersion freezing starting at
15 -28.5°C . This might be due to the spores being coated with hydrophobic proteins that are widespread in filamentous fungi such as *Cladosporium* sp. Additionally, fungal aerosols are likely to be effective cloud condensation nuclei, but data on behalf of this is still scarce.

Recent field measurements have highlighted the importance of bioaerosols as ice
20 nucleators in the atmosphere, e.g. Pratt et al. (2009) and Prenni (2009). Relying on the above evidence, there is probably a link between meteorological conditions and fungal spores as well. On the one hand, fungal spores acting as ice nuclei might influence cloud and precipitation formation process, as has already been proposed by Morris et al. (2004) in general for biological ice nuclei. On the other hand, changes in climatic
25 conditions also alter the meteorological situation on a smaller time scale which in turn might influence fungal spore release as well as transport according to the respective release mechanism. These possible interactions with the weather and climate system as well as the fact that fungi are one of the major contributors to global bioaerosols makes it crucial to gain more knowledge about the circumstances and amounts in

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which they are emitted as well as their transport behaviour. Many studies have already focused on sampling of fungal spores in order to estimate their concentration in the atmosphere. However, a standardised procedure in order to do so is still missing which leads to very heterogeneous and hardly comparable results.

5 The goal of this paper is to review the available literature data on fungal spores and estimate global fungal spore emissions by biome area. Available literature is reviewed and data provided used to derive the respective fungal spore fluxes for major ecoregions. Moreover, measurement methods are reviewed and discussed.

2 Data and Methods

10 A review of available fungal spore concentration data has been undertaken. Fungal spore concentration data have been assigned to an ecosystem and converted to surface number and mass fluxes. More than 150 studies have been reviewed of which 35 have been found to contain data relevant for this study, and thus were taken into account for flux calculations.

15 The biome areas by Olson et al. (2001) have been used for ecosystem classification. But since data points were not sufficiently dense, broader definitions of the respective biomes had to be taken. These ecoregions covered forest, shrub, grass, crop, tundra and land ice (data based on (World Resource Institute, 2003a,b)). Attribution of the respective ecoregions by Olson et al. (2001) to the biome areas used here has been
20 done according to Table 1. The biome “crop” was used when the studies mentioned close proximity to agriculture land. Effects of urban environments were not taken into account. Biome area data has been derived from World Resource Institute (2003a,b). Figure 1 shows the global distribution of available measurement data.

Fluxes have been calculated based on ecosystem areas and fungal spore properties:

$$25 F_{\text{fungal spore}} = \frac{\text{ecosystem area} \times \text{number concentration} \times \text{spore mass} \times \Delta\rho}{\text{total earth area} \times g \times \text{air density}} \quad (1)$$

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Alternative approaches to calculate fungus fluxes have been derived for instance by Heald and Spracklen (2009) and used by Hoose et al. (2010):

$$F_{\text{fungal spores}} = 500\text{m}^{-2}\text{s}^{-1} \frac{\text{LAI}}{5} \frac{q}{1.5 \times 10^{-2}\text{kgkg}^{-1}} \quad (2)$$

where LAI is the leaf area index, a measure for the leaf area per surface area and q is the specific humidity. The second of the two flux calculation methods has not been used since the LAI is not necessarily a good measure of spore emissions, as it would create a bias towards too low fungal spore fluxes in regions where the LAI is very low, such as grasslands.

Spore masses have been derived by Winiwarter et al. (2009): Assuming an average carbon content of 13 pg C per spore (Bauer et al., 2002a,b), a water content of 20% per spore and 50% C per dry mass (Sedlbauer and Krus, 2001) they determined a fungal spore mass of 33 pg. Calculations by Elbert et al. (2007) resulted in remarkably higher values: assuming a mass density of about 1gcm^{-3} and a volume equivalent diameter of about $7\text{ }\mu\text{m}$, the average mass of wet spore discharging Ascomycota would be around 200 pg. Assuming the same density for Basidiomycota, Elbert et al. (2007) derived a mass of 65 pg.

For calculation of mass fluxes in this paper, the average mass of 33 pg per spore has been assumed. The number and mass fluxes are listed once per second and once per second and square meter of the specific biome. Global averages are derived by taking the mean of the respective values for each biome area.

The following assumptions have been made for the flux calculations:

- Seasonal or daily cycles do not influence the measured spore concentrations.
- There is no difference between colony forming units (CFU) and total counts.
- The biome region forest comprises all types of forests regardless of the prevailing vegetation types.
- Similar assumptions have been made for the other biome regions.

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Best estimates have been calculated from all average spore concentration data available. Lau et al. (2006) are the only researchers that have expressed their data with the geometric mean instead of the arithmetic mean. Since the difference between the geometric mean and the arithmetic mean are small, they have been treated in the same manner. It should be noted that for the low and high estimates of crop emissions, only one measurement result was available. Where no average concentrations were provided, the average between the maximum and minimum spore concentrations (if available) has been taken instead. The high and low estimates are the averages of all minimum and maximum spore counts (where available). In the optimum case, total spore counts were provided covering all identifiable species. However, in some studies, only certain genera were investigated. Where spore counts had been split according to species, the sum over all has been taken in order to get as close as possible to the number of total counts.

Table 2 shows the aggregated number fluxes of fungal spores per square metre of biome and second, while Table 3 shows the respective mass fluxes in kg per square metre and second. The biome area with the largest fungal spore flux is crop followed by shrub, forest, grassland and tundra in descending order. This can also be seen in Fig. 2, showing the fungal number flux, which was produced by combining the best estimates of reviewed fungal spore data with the plant functional types from the JSBACH dynamic vegetation model (Raddatz et al., 2007).

As for the prevalence of different spore genera, most of the studies agree that *Cladosporium* make up a very dominant part of the fungal spore air spora, e.g. Sakiyan and Inceoglu (2003); Mallo et al. (2010). Other species such as *Alternaria*, *Aspergillus*, *Ganoderma*, *Agaricus*, *Coprinus*, *Leptosphaeria* or smuts and rusts have been considered as important constituents, but usually showed much lower concentrations than *Cladosporium* (e.g. (Sakiyan and Inceoglu, 2003; Mallo et al., 2010). Goncalvez et al. (2010) concluded based on literature studies that *Asperigllus*, *Alternaria* and *Penicillium* were predominant in hot climates, whereas *Cladosporium* spores were found to be most abundant in temperate climatic regimes.

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2.1 Review of measurement methods

The simplest method to measure airborne fungal spores is to expose sticky surfaces or petri dishes and then count either all detectable fungal spores or, in the case of petri dishes, the colony forming units (CFU). This method has for instance been used by Bhati and Gaur (1979) or Abu-Dieyeh et al. (2010). The obtained sample results are useful in order to get a qualitative impression of the composition of the prevailing air spora. However, Gregory (1952) pointed out that these data imply the “tacit assumption that the relation between the number of particles suspended in the air flowing over the surface and the number deposited on the surface is known”. Gregory (1952) further argue that these simple rules would only apply for still air. According to the authors of the study, the efficiency of a sticky surface to collect fungal spores rather varies with wind speed and subsequently number concentrations per unit volume are difficult to obtain. Gregory (1952) note, that a good sampling device draws in “a known volume of air without altering its spore content, removes all particles over the 2–100 μm size range, and leaves them in a form in which they can be examined, counted and classified”.

Hirst (1952) described the features a measurement device should have in order to give useful results: Besides the ability of assessing the spore concentration per unit volume of air, it should also be possible to measure in distinct time intervals to better correlate concentrations with meteorological conditions. He designed a spore trap that was able to suck in air and subsequently impact the contained spores on a sticky surface. The principle of suction increases, as Hirst (1952) argues, the efficiency of filtration and impaction. However, he also found that this does not guarantee for the air masses entering the trap being representative of the actual spore load (collection efficiency). To counteract this problem, Hirst (1952) proposed that air should be sampled isokinetically and that the orifice should always be directed into the air-stream. In order to get a distinction in time, a sticky slide is moved slowly past the orifice (Hirst, 1952). As suction rates are constant, trapping efficiencies change with wind speeds (Hirst, 1953).

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Recent methods take advantage of biochemical properties of fungal spores. Elbert et al. (2007) for instance use Ergosterol (a component of fungal cell membranes) as a fungal biomarker to determine their prevalence in air masses. Bauer et al. (2008) rely on other biochemical tracers such as mannitol or arabitol to measure the fungal spore content in the precipitation.

A review of the available studies of spore concentrations showed that the measurement methods applied were diverse. As outlined above, data from measurements with petri dishes have not been included in the flux calculations for this paper due to the above named reasons. The trapping efficiency of petri dishes is no higher than 5% which is remarkably lower than the 80% trapping efficiency of a Hirst trap (Davies et al., 1963, citing Gregory and Stedman 1953).

Among the data sets used for calculations, many of the researchers relied on the Hirst-type spore trap as described above, e.g. (Davies et al., 1963; Hamilton, 1959; Rodríguez-Rajo et al., 2005; Oliveira et al., 2009; Mallo et al., 2010; Levetin and Dorsey, 2006; Herrero et al., 2006; Wu et al., 2004; Stepalska and Wolek, 2009; Kasprzyk and Worek, 2006; Sakiyan and Inceoglu, 2003). Among these, mostly models from Lanzoni (VPPS 2000) (Lanzoni, 2010) or Burkard (Burkard Scientific, 2000) were used. Others relied on Filterhousings containing 2 μm filter membranes, e.g. Prospero et al. (2005); Griffin et al. (2001, 2003, 2007), for their measurement. Another device sometimes used was the May Cascade Impactor (May, 1945). However, this device was found to have a considerably lower trapping efficiency for small spores than the Volumetric Spore Trap (Hirst, 1953). Only a few of the studies monitored the fungal spore content in cloud droplets or precipitation (Amato et al. (2007); Bauer et al. (2002a)) and some other measurement devices and methods apart from those named above have been used as well (for detailed information on measurement methods see Table A1 in the appendix).

The measurement duration varied from a few minutes to continuous measurements seven days a week (especially applied for the Hirst-type spore traps). Also the time span over the year varied from study to study: some only measured on one single day,

e.g. Côté et al. (2008), others even over several years continuously, e.g. Mallo et al. (2010).

Besides the heterogeneity of the used measurement devices also the airflow varied from 1.9 l/min (Griffin et al., 2001) up to 1.13 m³/min (Lau et al., 2006). An airflow of 10 l/min seems to be the most commonly used value for such measurements. Moreover it was difficult to retract the airflow rates from all studies. The correct choice of airflow is an important factor for spore measurements since measurements that are not conducted isokinetically can lead to remarkable biases in spore counts.

Furthermore the height at which the devices had been installed was not the same in the respective studies. Some used air samples in heights up to several kilometres, whereas other conducted ground-based measurements in heights from 2 m up to 50 m. When considering spore dispersal from a boundary layer meteorological point of view, the choice of the measurement height might be crucial since it decides on whether measurements are taken within or outside the turbulent layer.

The situation is alike for the different impaction media chosen: whereas those using the Lanzoni Hirst-type spore trap rely on so-called Melinex tape which is mounted after spore collection with glycerol jelly, others use different surfaces. The same situation can be found when it comes to the use of nutrient media for growth of the trapped fungal spores (viable counts). Some rely on R2A agar, others on YM (yeast-morphology) agar, others on Sabouraud's medium for fungi or malt-agar extract, etc. The possibilities for fungus incubation for viable counts are numerous. Incubation times vary from two days up to two weeks and longer and so do also the incubation temperatures applied. Moreover, counting methods are not the same in all studies. Some use optical methods such as microscopy or macroscopy with different magnifications (ranging from 40x-1000x) while others use Polymerase Chain Reaction (PCR) to determine genera and species from their genome. As for the nutrient medium chosen, Griffin et al. (2007) point to two studies both concluding that the choice of nutrient medium had an influence on the prevalence of respective species counted.

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To sum up, the measurement methods differ at many stages of the measurement and counting process: The counting device, the airflow chosen, the placement of the sampling device, the sticky medium, the nutrient medium (for viable counts), the incubation duration and the counting method. It is crucial to introduce a convention on how to exactly measure fungal spores in the atmosphere in order to prevent biases due to different measurement methods and to increase comparability of results.

2.2 CFU vs. total spore count

Not all studies have investigated both the total count of all spores available and the counts of viable spores called colony forming units (CFU) after incubation. However, this would be an important source of information on what share of the atmospheric fungal spora is viable and which is not (Gregory, 1967). In very few of the studies, both the viable and total counts of spores have been investigated, e.g. Lau et al. (2006); Pady and Kapica (1955); Griffin et al. (2001); Bauer et al. (2002a). All other studies either published total spores or only CFUs. In order to assess their activity as CCN or IN it is not relevant whether they are alive or not. The important feature is the shape and presence of the active proteins which actually act as nuclei. Therefore it is all the more important to evaluate total counts instead of viable counts in order to include all possible IN.

Pady and Kapica (1955) found that silicone slides exposed in a slit sampler revealed spore counts a manifold higher than those of plates exposed at the same time where CFUs had been counted. This could be explained by a remarkable bias between viable and total spore counts. Gregory (1967) found that viability of *Alternaria* spores averaged at 80% and that of *Cladosporium* spores at 42% with viability decreasing at midday. Hence, viability varies from species to species. Other sources report *Cladosporium* viability to be on average at 62% (Pady and Gregory, 1963). Experiments by Harvey (1967) investigated viability of *Cladosporium* and came to the conclusion that single spores germinate more readily than clumps of spores. Moreover they also found a diurnal cycle in germination that reached maximum values between 10:00 UTC and

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18:00 UTC and minimum values at 02:00 UTC. However, the authors also state that this cyclicity of viability is in disagreement with the findings by Pathak and Pady (1965). Bauer et al. (2002a) estimated the total viability of the sampled bacteria and fungi to be around 87% using the condition of the cell wall as a criterion to determine viability.

5 Analysis of snow samples then showed that the cultivable part of fungi amounted only up to 0.7% (Bauer et al., 2002a). This seems a very low number, but it is sensible considering the fact that these spores already had to survive very harsh conditions within the ice crystals or even during precipitation formation processes. Fisar et al. (1990) compared two counting methods, CFUs and direct counts (Fluorescence technique; see respective paper for detailed description of this method) and came to the conclusion that the difference between CFUs and direct counts for both, bacteria and yeasts, is not only considerable but also highly variable. The authors added that seasonal trends in these discrepancies were not detected.

10 The information provided in the above section is strong evidence for the fact that CFU counts and total spore counts are not equal at all. Due to the scarcity of studies including both viable and total counts, values for CFUs and total spore counts have been treated equally in this paper knowing that the two counting methods show remarkable differences in resulting counts.

3 Discussion

20 The fungal spore fluxes for the respective biome areas are in the expected orders of magnitude. The more a biome region is vegetated, the higher are the fungal spore emissions (cf. Table 2 and Fig. 2). This makes sense considering the fact that plants are the largest source of fungal bioaerosol. This reasoning is also supported by Heald and Spracklen (2009), although their fungal spore flux calculations are based on the leaf area index (LAI) which might result in a bias towards too low emissions for biomes with lower LAI as already pointed out in chapter 2.

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Unfortunately, no useful data in land ice areas were found so that emissions are not available for this ecoregion. It would nonetheless be worth investigating these regions as well. Lichen soredia (i.e. the reproductive structure of lichen) have been reported to be most abundant in maritime Antarctica (Henderson-Begg et al., 2009, citing Marshall 1996). Considering the fact that lichen have been found to be effective ice nuclei, it is probable that lichen in these ecoregions do have an influence on cloud microphysical processes as well as precipitation formation. A number of studies mainly focused on species such as *Cladosporium*, *Aspergillus* or *Alternaria*. This is mainly because these fungi can cause allergies (Goncalvez et al., 2010, citing Vijay 2005 and Shen 2007).

Heald and Spracklen (2009) conducted an estimate of fungal spore emissions based on mannitol concentrations (a biotracer for fungi) using the GEOS-chem chemical transport model (see respective paper for detailed information). Two major differences between the respective results can be seen in the tropical regions. Whereas Heald and Spracklen (2009) found highest values in the Amazon and tropical African region, the present study does not reveal maximum values in these regions. Moreover, mass fluxes found by Heald and Spracklen (2009) are with $5.96 \times 10^{-12} \text{ kgm}^{-2} \text{ s}^{-1}$ an order of magnitude higher than those presented here (cf. Table 4), as are the values by Elbert et al. (2007) with $3.62 \times 10^{-12} \text{ kgm}^{-2} \text{ s}^{-1}$. Nevertheless, the values presented here ($4 \times 10^{-13} \text{ kgm}^{-2} \text{ s}^{-1}$ best estimate, cf. Table 4) are in agreement with the study by Winiwarter et al. (2009), who calculated global average fungal spore emissions of $5.71 \times 10^{-13} \text{ kgm}^{-2} \text{ s}^{-1}$.

The lower values found in tropical regions can partly be explained by the fact that fungal spore data from forests have been aggregated up to one biome area irrespective of forest type. Both methods are prone to biases and errors. The downsides of the present method will be outlined in chapter 3.1. However, it is also likely that the results by Heald and Spracklen (2009) are based on different assumptions. As outlined in chapter 1 fungal spore composition and size can be very heterogeneous and variable. Nevertheless, the approach of Heald and Spracklen (2009) is promising as seasonality and meteorological influences have been taken into account.

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Probably the measurements of actual spore concentrations as well as the measurements of biological tracer substances to derive fungal spore fluxes have to be seen in a complementary way. Concentration measurements on the one hand yield absolute counts of all fungal spores, but comprise measurement issues outlined in previous chapters as well as some problems with the identification of fungal spores. As for the biochemical tracer method, these problems are not encountered, but more knowledge needs to be gained in terms of chemical composition of primary biological aerosols as to better describe them and hence yield more accurate results. Therefore it is useful to intercompare the two approaches in order to determine possible sources of error and strengthen hypotheses where agreement is achieved.

3.1 Sources of error

As mentioned above, the results of this study have to be taken with caution. The density of measurement points was not sufficient to take into account all ecosystems and therefore only a very coarse distinction into the here presented biome areas could be made. This also implies that a tropical broadleaf forest is considered to emit the same amount and kind of spores as a coniferous forest in higher latitudes. This of course does not make sense from a biological point of view. Moreover, the seasonal and diurnal cycles which clearly have been detected (see chapter 2) could not be taken into account due to scarcity of data. The fact that the difference between CFUs and total counts is not considered clearly must bias the results especially since only very little information is available on what share of fungal spores are viable.

The present data have been calculated on the basis of many simplifications and assumptions that had to be made due to the scarcity of data. As outlined in chapter 2, also measurement methods showed high heterogeneity which can clearly be regarded as a source of bias in the present dataset. Nevertheless it is a first step towards enumerating fungal spore concentrations and fluxes on a global basis.

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3.2 Outlook

In order to minimise the above named sources of error, measurement methods need to be standardised in order to allow for better comparability. Furthermore, results should always comprise both CFU and viable count data. To allow for a finer resolution of flux data, data points should be distributed more densely and represent a larger set of investigated ecosystems. In order to account for seasonal and daily cycles, measurements should be continuous over periods at least lasting a full year.

Since investigation of bioaerosols in general is highly interesting due to their possible influence on cloud microphysical processes, further research would be needed to learn more about the potential of fungal spores to act as CCN or IN. Moreover, lichen which have been reported to be effective IN should be investigated better since they are more abundant in the atmosphere than bacteria (Henderson-Begg et al., 2009). Additionally, data should not only focus on allergy causing fungi, but also on those spores which presumably influence atmospheric processes. It would therefore also make sense to investigate concentrations of IN active spores such as *Fusarium* in order to get a broader picture of what share of all fungal spores is actually involved in ice crystal formation processes.

4 Conclusions

The present study has reviewed data and information available on fungal spore concentrations and derived fungal spore emissions. As outlined above, data quality in general is rather poor due to the heterogeneity of the applied measurement methods as well as the quality of the measurements themselves. A standardized measurement method would be of help in order to minimize measurement biases and allow for better inter-comparability of measurements. The resulting global emission flux of fungal bioaerosol of $4 \times 10^{-13} \text{ kg m}^{-2} \text{ s}^{-1}$ was proven to be in agreement with previous studies. Despite manifold sources of error, the calculated fluxes can be considered as a good first result.

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This could provide a basis for further research on fungal spore emissions depending on biome area. The resulting fluxes are useful in order to evaluate the impact of global fungal aerosol on weather and climate.

Appendix A

Overview of measurement methods and observational data

The following tables comprise information on measurement methods employed by the respective studies (see Table A1) as well as all the values used for flux calculations (see Table A2). Multiple values for the same source can occur in case multiple measurements over different intervals of time had been undertaken or different sites had been chosen for measurement. These cases were treated as single measurement points.

Acknowledgement. The authors would like to thank Ulrike Lohmann and Trude Storelvmo for valuable feedback on this paper.

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Ecoregion after Olson et al. (2001)	Biome area
Tropical and Subtropical Moist Broadleaf Forests	Forest
Tropical and Subtropical Dry Broadleaf Forests	Forest
Tropical and Subtropical Coniferous Forests	Forest
Temperate Broadleaf and Mixed Forests	Forest
Boreal Forests/Taiga	Forest
Tropical and Subtropical Grasslands, Savannas, and Shrubland	Shrub
Temperate Grasslands, Savannas, and Shrubland	Shrub
Flooded Grasslands and Savannas	Shrub
Montane Grasslands and Shrubland	Shrub
Mediterranean Forests, Woodlands, and Shrubs	Shrub
Tundra	Tundra
Desert and Xeric Shrublands	Grassland

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Biome	low estimate	best estimate	high estimate
Forest	1.77	3.13	22.9
Shrub	0.72	24.7	67.5
Grassland	0.14	1.45	10.6
Crop	31.3	31.8	33.2
Tundra	0.01	0.03	0.06

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Table 3. Mass fluxes of fungal spores per square metre of biome and second [$\text{kgm}^{-2}\text{s}^{-1}$].

Biome	low estimate	best estimate	high estimate
Forest	5.88×10^{-14}	1.04×10^{-13}	7.57×10^{-13}
Shrub	2.37×10^{-14}	8.15×10^{-13}	2.23×10^{-12}
Grassland	4.53×10^{-15}	4.77×10^{-14}	3.51×10^{-13}
Crop	1.03×10^{-12}	1.05×10^{-12}	1.10×10^{-12}
Tundra	1.73×10^{-16}	1.01×10^{-15}	1.85×10^{-15}

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**Table 4.** Global average number [$\text{m}^{-2}\text{s}^{-1}$] and mass [$\text{kgm}^{-2}\text{s}^{-1}$] fluxes of fungal spore emissions.

	low estimate	best estimate	high estimate
number flux	6.78	12.2	26.9
mass flux	2.24×10^{-13}	4.03×10^{-13}	8.87×10^{-13}

Table A1. Sources used for fungal spore flux calculations and details about their measurement procedure.

Source	Sampling Device	Airflow	Sample Period/Number of Samplings
Amato et al. (2005)	Single stage cloud collectors	n/a	2 Samplings
Amato et al. (2007)	Sterilised cloud droplet impactor	n/a	7 cloud events
Bauer et al. (2002a)	Active cloud water sampler	n/a	3 cloud events, 8 samplings
Beaumont et al. (1985)	Andersen Sampler model 0101	28.3 l/min	1981–1983/weekly, 3 samplings per day
Burch and Levetin (2002)	Burkart volumetric spore trap	n/a	four days in September
Côté et al. (2008)		12.5 l/min	6.5 h/one sampling
Davies et al. (1963)	Hirst-type spore trap	10 l/min	n/a
Herrero et al. (2006)	Hirst-type spore trap (Burkart)	n/a	year 2003/continuous samplings
DiGiorgio et al. (1996)	Hirst-type spore trap (Burkart)	40 l/min	one year/2 samplings a week
Elbert et al. (2007)	Rotating impactor, isokinetic jet impactor	n/a	2001/continuous measurements
Fisar et al. (1990)	Single stage large-volume impactor	42 l/min	50–200 l per sample, i.e. a few minutes
Glikson et al. (1995)	Teflon filters for PM10	n/a	4–8 1992/daily samplings
Gregory (1952)	May cascade impactor	10 l/min	24 h
Griffin et al. (2001)	Filter samples	9.3 l/min	18–28 July 2000 5 samplings
Griffin et al. (2003)	Filter membrane	6.5–28.4 l/min	18 July 2000–8 August 2001
(Griffin et al., 2006)	Filter membrane	1.9–17.4 l/min	06:30–18:45 UTC/2–3 air samplings
Griffin et al. (2007)	Membrane Filtration	n/a	3–10 2002/continuous samplings
Griffin (2007)	Data taken from multiple sources		
Hamilton (1959)	Hirst-type spore trap	10 l/min	5–9 1954/15 min per day
Ho et al. (2005)	Hirst-type spore trap	10 l/min	continuous from 1993 to 1996
Kasprzyk and Worek (2006)	Hirst-type spore trap (Lanzoni)	10 l/min	one year/continuous samplings
Kellogg et al. (2004)	in-house designed system	10 l/min	
Lau et al. (2006)	Graseby GMWT 2200	1.13 m ³ min ⁻¹	8–12 2002/weekly samples (72 h)
Levetin and Dorsey (2006)	Hirst-type spore trap (Burkart)	n/a	2002/daily samplings
Mallo et al. (2010)	Hirst-type spore trap (Lanzoni)	10 l/min	1998–2001 continuous samplings
Marks et al. (2001)	Sartorius MD-8 air filtration unit	0.5–1 m ³	2nd–5 July 97 and 2nd–14th 98
Oliveira et al. (2009)	Hirst-type volumetric spore trap	10 l/min	2005–2007/continuous samplings
Pady and Kapica (1955)	Bourdillong slit sampler and McGill GE	28.3 l/min	2 sampling flights Montréal-London
Prospero et al. (2005)	Filter Samples	10 l/min	1996–1997/continuous samplings
Rodríguez-Rajo et al. (2005)	Hirst-type spore trap (Lanzoni)	10 l/min	whole year/continuous samplings
Sabariego et al. (2000)	Hirst-type spore trap (Burkart)	10 l/min	whole year/continuous samplings
Sakiyan and Inceoglu (2003)	Hirst-type spore trap (Burkart)	10 l/min	whole year/continuous samplings
Simeray et al. (1993)	S.A.S. Sampler	0.15 m ³	1989–1990, 100 s per sample/once a week
Stepalska and Wolek (2009)	Hirst-type spore trap	10 l/min	Daily average concentrations 1997–1999
Winiwarter et al. (2009)	Data taken from multiple sources		
Wu et al. (2004)	Hirst-type spore trap (Burkart)	10 l/min	12 2000–04 2001/continuous sampling
Wu et al. (2007)	Portable air samplers for agar plates	20 l/min	03 2003–12 2004, 2 min/sample/2x monthly

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Table A2. Data used as input for fungal spore flux calculations.

Source	Ecosystem	Average conc.	Min conc.	Max. conc.	Average flux	Min flux	Max flux
Amato et al. (2005)	Forest	221.5	53	390	18.81583418	4.502208631	33.12945973
Bauer et al. (2002a)	Forest	2200	340	5000	186.8841318	28.8820931	424.7366633
Bauer et al. (2002a)	Forest	1200	170	3200	101.9367992	14.44104655	271.8314645
Bauer et al. (2002a)	Forest	346	49	863	29.3917771	4.1624193	73.30954808
Beaumont et al. (1985)	Forest	258			21.91641182		
Burch and Levetin (2002)	Shrub	50000			4247.366633		
Côté et al. (2008)	Forest	615.35	492.3	738.4	52.27234115	41.81957187	62.72511043
Herrero et al. (2006)	Shrub	609.2			51.74991505		
DiGiorgio et al. (1996)	Shrub	92			7.815154604		
DiGiorgio et al. (1996)	Shrub	46			3.907577302		
Elbert et al. (2007)	Forest	12476	4764	20188	1059.802922	404.6890928	1714.916752
Fisar et al. (1990)	Forest	17			17.1593612		
Gregory (1952)	Crop	9175			779.3917771		
Gregory (1952)	Crop	11900			1010.873259		
Gregory (1952)	Crop	6975			592.5076453		
Gregory (1952)	Crop	9372			796.1264016		
Gregory (1952)	Crop	13970			1186.714237		
Gregory (1952)	Crop	9830			835.03228		
Gregory (1967)	Forest			43300			3678.219504
Gregory (1967)	Forest			5250			445.9734964
Gregory (1967)	Forest	76			65.06965681		
Griffin et al. (2001)	Grassland	42			0.056185277		
Griffin et al. (2001)	Forest	14.286			0.077221593		
Griffin et al. (2003)	Forest	0.0175			1.486578321		
Griffin et al. (2003)	Forest	57			4.841997961		
Griffin et al. (2003)	Forest	8.625	5	20	0.732670744	0.424736663	1.698946653
Griffin et al. (2003)	Forest	12	8	24	1.019367992	0.679578661	2.038735984
Griffin et al. (2003)	Grassland	24			2.038735984		
Griffin et al. (2003)	Grassland	46.25	27	57	3.928814135	2.293577982	4.841997961
Griffin et al. (2003)	Grassland	64.667	48	90	5.493260845	4.077471967	7.645259939
Griffin et al. (2003)	Grassland	11.33	8	14	0.962736437	0.679578661	1.189262657
Griffin et al. (2007)	Grassland	869			73.81923208		
Griffin et al. (2007)	Grassland	215	205	226	18.26367652	17.41420319	19.19809718
Griffin et al. (2007)	Shrub	73	31	115	6.201155284	2.633367312	9.768943255
Griffin et al. (2007)	Grassland	66	0	703	5.606523955	0	59.71797486
Griffin et al. (2007)	Shrub	25	0	291	2.123683316	0	24.7196738
Griffin et al. (2007)	Grassland	3	0	27	0.254841998	0	2.293577982
Griffin et al. (2007)	Grassland	1398	336	6992	118.756371	28.54230377	593.9517499
Griffin et al. (2007)	Forest	1702	100	8510	144.5803602	8.494733265	722.9018009
Hamilton (1959)	Crop	14800			1257.220523		
Hamilton (1959)	Crop	8200	6400	10000	696.5681278	543.662929	849.4733265
Ho et al. (2005)	Grassland	6078			516.3098879		
Ho et al. (2005)	Grassland	4839			411.0601427		
Ho et al. (2005)	Grassland	6078			516.3098879		
Ho et al. (2005)	Forest	4839			411.0601427		
Kasprzyk and Worek (2006)	Forest	2144.4			182.1590214		

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Table A2. Continued.

Kasprzyk and Worek (2006)	Forest	2183.2			185.4553177			
Kasprzyk and Worek (2006)	Forest	2092.6			177.7601087			
Kasprzyk and Worek (2006)	Forest	2145.7			182.2738702			
Katial et al. (1997)	Shrub	409			1.590015258			
Kellogg et al. (2004)	Grassland	225	80	370	19.11314985	6.795786612	31.43051308	
Kellogg et al. (2004)	Grassland	65	0	130	5.521576622	0	11.04315324	
Kellogg and Griffin (2006)	Grassland	0			0			
Kellogg and Griffin (2006)	Grassland	60			5.096839959			
Lau et al. (2006)	Forest	86	18	341	0.97028931	0.097299207	1.843279414	
Lau et al. (2006)	Forest	72	30	294	0.87569286	0.162165344	1.589220375	
Lau et al. (2006)	Forest	292	7	2386	24.80462113	0.594631329	202.6843357	
Lau et al. (2006)	Forest	247	50	1540	20.98199117	4.247366633	130.8188923	
Levetin and Dorsey (2006)	Shrub	24121	53	48188	2048.972137	4.502208631	4093.442066	
Levetin and Dorsey (2006)	Shrub	5459.4		64363	463.7614679		5467.465172	
Mallo et al. (2010)	Shrub	284.51		2000	24.16836561		169.8946653	
Mallo et al. (2010)	Shrub	814.43		3488	69.18365613		295.4918451	
Marks et al. (2001)	Forest	105	0	1000	8.919469929	0	84.94733265	
Marks et al. (2001)	Forest	223	0	600	18.94325518	0	50.96839959	
Marks et al. (2001)	Forest	26	0	200	2.208630649	0	16.98946653	
Marks et al. (2001)	Forest	12	0	45	1.444104655	0	3.822629969	
Oliveira et al. (2009)	Forest	531		8509	45.10703364		722.8168536	
Oliveira et al. (2009)	Shrub	934		8761	79.3408087		744.2235814	
Pady and Kapica (1955)	Forest	36.55	6.0035	67.1	3.104865957	0.509977983	5.69975393	
Pady and Kapica (1955)	Forest	229.9	170.22	289.6	19.52915689	14.45937576	24.59893801	
Pady and Kapica (1955)	Forest	6.0035	6.0035	6.0035	0.509977983	0.509977983	0.509977983	
Pady and Kapica (1955)	Forest	43.79	38.846	48.73	3.719839407	3.299857539	4.139821276	
Pady and Kapica (1955)	Tundra	30.37	4.2377	56.5	2.579888621	0.359984459	4.799792783	
Pady and Kapica (1955)	Tundra	86.52	14.126	158.9	7.349682699	1.199948196	13.4994172	
Pady and Kapica (1955)	Tundra	3.0017	1.7657	4.238	0.254988992	0.149993524	0.359984459	
Pady and Kapica (1955)	Tundra	38.846	7.0629	70.63	3.299857539	0.599974098	5.999740979	
Pady and Kapica (1955)	Forest	16.245			1.379940425			
Pady and Kapica (1955)	Forest	30.724			2.609887326			
Pady (1957)	Shrub	24499	836.95	48162	2081.160152	71.0969306	4091.223374	
Pady (1957)	Shrub	715.12	169.51	1261	60.74737741	14.39937835	107.0953765	
Prospero et al. (2005)	Grassland	0.36			0.03058104			
Prospero et al. (2005)	Forest	92			7.815154604			
Prospero et al. (2005)	Forest	213			18.09378186			
Rodriguez-Rajo et al. (2005)	Forest	564.15			47.92263043			
Rodriguez-Rajo et al. (2005)	Shrub	950.24			80.72067921			
Rodriguez-Rajo et al. (2005)	Shrub	979.27			83.18624645			
Sabariego et al. (2000)	Shrub	831.8			70.65942403			
Sakiyan and Inceoglu (2003)	Shrub	2916.7	16.667	5817	71.02446483	1.415788878	494.1103183	
(Stepalska and Wolek, 2009)	Forest	3121			265.1206252			
Winiwarter et al. (2009)	Forest	49.315			4.189183528			
Wu et al. (2004)	Crop	28684			2436.609752			
Wu et al. (2004)	Grassland			29038			2466.728678	
Wu et al. (2007)	Forest	2233.2			189.7009854			
Wu et al. (2007)	Forest	2277.7			193.4811417			

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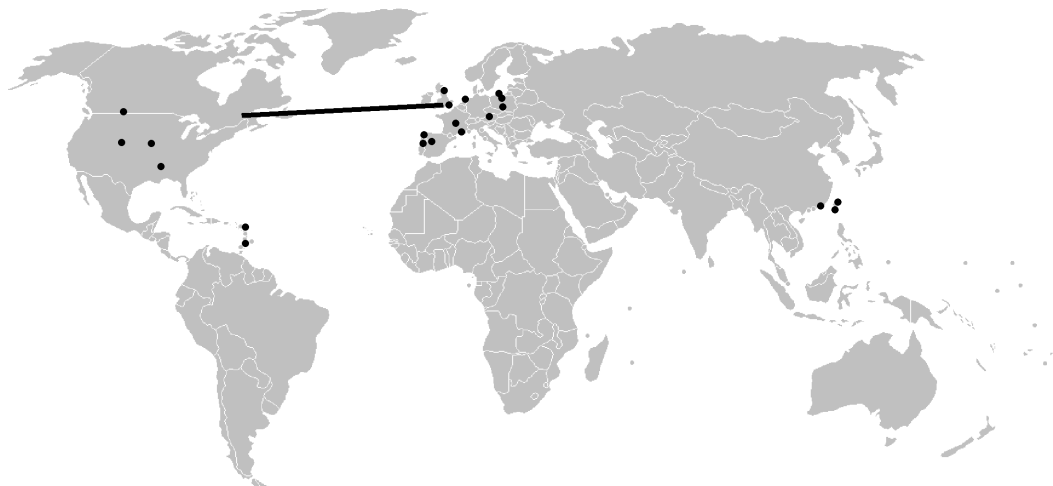
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Fig. 1. Global distribution of locations where fungal spore emissions have been measured. The transect over the ocean denotes ship measurements.

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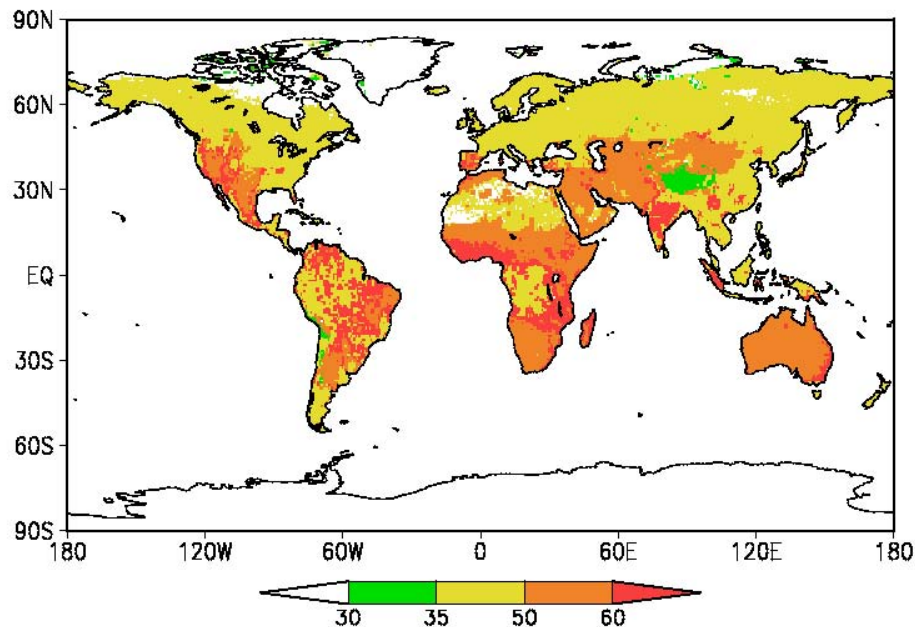


Fig. 2. Annual mean fungal spore number flux in $\text{m}^{-2} \text{s}^{-1}$.

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