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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 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 194 for tropical and subtropical forests, 203 for all other forests, 1203 for shrub, 2509 for crop, 8 for tundra, and 165 for grassland. No data were found for land ice. The annual mean global fluxes amount to $1.69 \times 10^{-11}\,\mathrm{kg\,m^{-2}\,s^{-1}}$ as the best estimates, and $9.01 \times 10^{-12}\,\mathrm{kg\,m^{-2}\,s^{-1}}$ and $3.28 \times 10^{-11}\,\mathrm{kg\,m^{-2}\,s^{-1}}$ 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 $\mathrm{m^{-3}}$, sometimes even exceeding 200 000 spores $\mathrm{m^{-3}}$ (Levetin, 1995). This is two orders of magnitude higher than observed peak pollen concentrations (1000–2000 grains $\mathrm{m^{-3}}$) (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. Elbert et al. (2007) found that fungal spores are the main contributor to the bioaerosol mass in the Amazon basin. Simulations conducted by 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. Fungi are even found in marine habitats where they are important decomposers of plant substrates (Hyde et al., 1998). As marine fungal spore emission observations are lacking so far, this biome has not been further taken account of in this review.

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, 2004; 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).

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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". The measured concentrations are a blend of local emissions and advected spores. It is difficult to distinguish between those two groups. A possible distinction criterion might be the size or shape since larger particles are deposited more easily than smaller ones. However, Heald and Spracklen (2009) note that the larger size fraction is less well investigated due to measurement device constraints. The farther away the sampling device is from the spore source, the more is the measured concentration influenced by deposition and other processes. This can lead to devices in immediate proximity to the ground measuring the actually emitted spore numbers, whereas other devices on higher levels might measure the escape fraction only. As most observational data was taken further away from the ground, we assume our estimate to represent 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 they are deposited either due to gravity, washout by rain or impaction (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.

Some fungal spores can act as very effective ice nucleators. Lichen were found to nucleate ice at temperatures higher than $-8\,^{\circ}\mathrm{C}$ and some even at temperatures higher than $-5\,^{\circ}\mathrm{C}$ (Kieft, 1988). The lichen fungus *Rhizoplaca chrysoleuca* was even found to be an active ice nucleus at temperatures as high as $-2\,^{\circ}\mathrm{C}$ (Kieft, 1988; Kieft and Ruscetti, 1990). To date, only a few fungus species have been found to be active 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. (2011) that showed poor ice nucleation ability of *Cladosporium* spores, with immersion freezing starting at $-28.5\,^{\circ}\mathrm{C}$. 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 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 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 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.

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

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. Exclusion criteria were a lack of information about measurement sites, biomes, measurement period, only absolute spore counts considered instead of concentrations, and petri dish samplings.

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 tropical and non-tropical forests, 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 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.

Table 1. Attribution of ecosystems by (Olson et al., 2001) to the respective biome areas

Ecoregion after Olson et al. (2001)	Biome	Area [km^{-2}]
Tropical and Subtropical Moist Broadleaf Forests	Tropical forest	
Tropical and Subtropical Dry Broadleaf Forests	Tropical forest	14 076 491
Tropical and Subtropical Coniferous Forests	Tropical forest	
Temperate Broadleaf and Mixed Forests	Forest	26 253 000
Boreal Forests/Taiga	Forest	
Tropical and Subtropical Grasslands, Savannahs, and Shrubland	Shrub	
Temperate Grasslands, Savannahs, and Shrubland	Shrub	
Flooded Grasslands and Savannahs	Shrub	23 343 164
Montane Grasslands and Shrubland	Shrub	
Mediterranean Forests, Woodlands, and Shrubs	Shrub	
Desert and Xeric Shrublands	Grassland	10 542 721
Crop	Crop	15 206 323
Tundra	Tundra	4 630 000

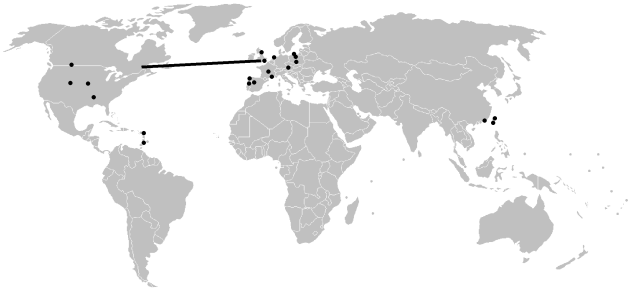

Fig. 1. Global distribution of locations where fungal spore emissions have been measured. The transect over the ocean denotes ship measurements.

Fluxes have been calculated based on fungal spore concentrations, the height (Δz) at which the spore concentration has been measured and the time (Δt) necessary for an uniform mixing of the atmospheric layer between ground and the height of the measurement:

$$F_{\text{fungal spore}} = \frac{\text{number concentration} \times \text{spore mass} \times \Delta z}{\Delta t} \quad (1)$$

Δz has been assumed to be 10 m. This is the average sampling height at which fungal spore concentrations have been measured, considering that sometimes samples have been taken at ground level, sometimes above tree level or on top of buildings. The height of 10 m for Δz is justified because it is at the top of the Prandtl layer in which fluxes between the ground and the atmosphere are constant with height (Colombe Siegenthaler-LeDrian and Tanja Stanelle, personal communication, 2011). We assume the concentration measured at this level to be in a steady state between spore emissions and dry deposition.

As the density of fungal spores is slightly lower than that of air, they are lifted with thermals and their dry deposition can be neglected for this offline calculation. This is supported by a terminal velocity of $v = 6.12 \times 10^{-7} \text{ms}^{-1}$ which can be derived assuming a fungal spore diameter of 10 µm and a density of 1kgm^{-3}.

The timescale for turbulent diffusion in the 10 m layer can be obtained from

$$\Delta t = \frac{(\Delta z)^2}{2 \times K_{\text{turb}}} = 50\text{s} \quad (2)$$

with $\Delta z = 10\,\text{m}$ and turbulence diffusion coefficient $K_{\text{turb}} = 10^5 \text{cm}^{-2}\text{s}^{-1}$ (Jacob, 1999).

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

$$F_{\text{fungal spores}} = 500\,\text{m}^{-2}\text{s}^{-1} \frac{\text{LAI}}{5} \frac{q}{1.5 \times 10^{-2}\text{kgkg}^{-1}} \quad (3)$$

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 $1\,\text{gcm}^{-3}$ and a volume equivalent diameter of about 7 µm, the average mass of wet spore discharged by 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

Table 2. Number fluxes of fungal spores per square metre of biome and second [m^{-2} s^{-1}].

Biome	low estimate	best estimate	high estimate
Tropical forest	93	194	458
Forest	31	214	387
Shrub	37	1203	3472
Grassland	14	165	1111
Crop	2469	2509	2549
Tundra	1	8	15

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

Biome	low estimate	best estimate	high estimate
Tropical forest	3.06×10^{-12}	6.40×10^{-12}	1.51×10^{-11}
Forest	1.02×10^{-12}	7.08×10^{-12}	1.28×10^{-11}
Shrub	1.22×10^{-12}	3.97×10^{-11}	1.15×10^{-10}
Grassland	4.65×10^{-13}	5.44×10^{-12}	3.67×10^{-11}
Crop	8.15×10^{-11}	8.28×10^{-11}	8.41×10^{-11}
Tundra	4.49×10^{-14}	2.62×10^{-13}	4.79×10^{-13}

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.
- Due to data scarcity the measurements taken at specific ecosystems were summarised in broader categories (cf. Table 1).
- Similar assumptions have been made for the other biome regions.

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, tropical and non-tropical forest, grassland and tundra in descending order. This can also be

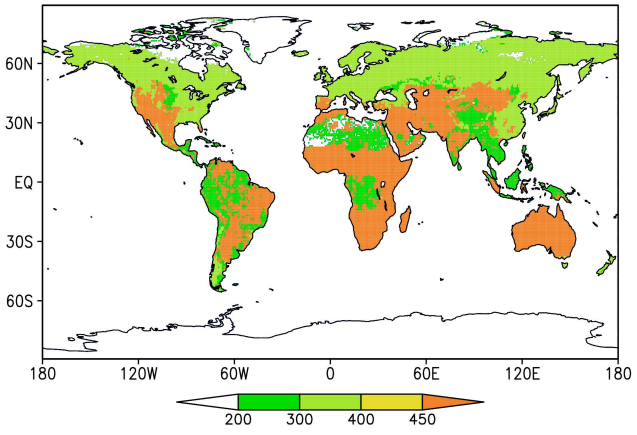

Fig. 2. Best estimate weighted annual mean fungal spore number flux in m^{-2} s^{-1}.

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). Based on literature studies, Goncalvez et al. (2010) concluded that *Asperigllus*, *Alternaria* and *Penicillium* were predominant in hot climates, whereas *Cladosporium* spores were found to be most abundant in temperate climatic regimes.

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 airstream. 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).

Recent methods take advantage of biochemical properties of fungal spores. Elbert et al. (2007) for instance use mannitol (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 $1.9\,\mathrm{l\,min^{-1}}$ (Griffin et al., 2001) up to $1.13\,\mathrm{m^3\,min^{-1}}$ (Lau et al., 2006). An airflow of $10\,\mathrm{l\,min^{-1}}$ seems to be the most commonly used value for such measurements. Moreover it was difficult to retrieve 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, both Abdel-Hafez et al. (1985) and Abdel-Hafez et al. (1986) conclude that the choice of nutrient medium had an influence on the prevalence of respective species counted.

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 (Kieft and Ruscetti, 1990). Therefore, it is not the viability of the fungal spore that affects its IN activity, but whether the ice nucleation active proteins on its surface are denatured or not. If the protein conformation is intact, it can trigger the ice nucleation, regardless of the cell's viability. However, it is important that the cell has been alive at one point in order to produce the ice nucleation proteins in the first place. Therefore it is all the more important to evaluate total counts instead of only viable counts in order to include all possible IN present on the spore surface.

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 18:00 UTC and minimum values at 02:00 UTC. However, the authors also state that this cyclicality 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. 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.

Table 4. Weighted average number [$m^{-2}s^{-1}$] and mass [$kgm^{-2}s^{-1}$] fluxes of fungal spore emissions over land.

	low estimate	best estimate	high estimate
number flux	273	513	995
mass flux	9.01×10^{-12}	1.69×10^{-11}	3.28×10^{-11}

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

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 Sect. 2.

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 $5.96 \times 10^{-12}\,\mathrm{kgm^{-2}s^{-1}}$ an order of magnitude lower than those presented here (cf. Table 4). (Winiwarter et al., 2009), who calculated global average fungal spore emissions of $5.71 \times 10^{-13}\,\mathrm{kgm^{-2}s^{-1}}$ came to values two orders of magnitude smaller. Nevertheless, the values presented here ($1.69 \times 10^{-11}\,\mathrm{kgm^{-2}s^{-1}}$, for best estimate cf. Table 4) are in agreement with the study by Elbert et al. (2007) that presents a fungal spore mass flux of $2.26 \times 10^{-11}\,\mathrm{kgm^{-2}s^{-1}}$.

The lower values found in tropical regions can partly be explained by the fact that fungal spore data for tropical 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 Sect. 3.1. However, it is also likely that the results by Heald and Spracklen (2009) are based on different asumptions. As outlined in Sect. 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.

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 sections 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 for example a deciduous 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 Sect. 2) could not be extended to all biomes and fungal species 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 Sect. 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 step towards enumerating fungal spore concentrations and fluxes on a global basis. We hope that our review will motivate further observations of fungal spore emissions, which might ultimately lead to an improved global database.

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

Table A1. Sources used for fungal spore flux calculations and details about their measurement procedure. Most samplings considered the total spore counts, those that considered only certain genera are indicated by the footnotes.

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	$28.3\,l\,min^{-1}$	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)		$12.5\,l\,min^{-1}$	6.5 h/one sampling
Davies et al. (1963)	Hirst-type spore trap	$10\,l\,min^{-1}$	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)	$40\,l\,min^{-1}$	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	$42\,l\,min^{-1}$	50–200l 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	$10\,l\,min^{-1}$	24 h
Griffin et al. (2001)	Filter samples	$9.3\,l\,min^{-1}$	18–28 July 2000 5 samplings
Griffin et al. (2003)	Filter membrane	$6.5–28.4\,l\,min^{-1}$	18 July 2000–8 August 2001
Griffin et al. (2006)	Filter membrane	$1.9–17.4\,l\,min^{-1}$	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	n/a	n/a
Hamilton (1959)	Hirst-type spore trap	$10\,l\,min^{-1}$	5–9 1954/15 min per day
Ho et al. (2005)	Hirst-type spore trap	$10\,l\,min^{-1}$	continuous from 1993 to 1996
Kasprzyk and Worek (2006)	Hirst-type spore trap (Lanzoni)	$10\,l\,min^{-1}$	one year/continuous samplings
Kellogg et al. (2004)	in-house designed system	$10\,l\,min^{-1}$	n/a
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)	$10\,l\,min^{-1}$	1998–2001 continuous samplings
Marks et al. (2001)	Sartorius MD-8 air filtration unit	$0.5–1\,m^3$	2–5 July 97 and 2–14 98
Oliveira et al. (2009)	Hirst-type volumetric spore trap	$10\,l\,min^{-1}$	2005–2007/continuous samplings
Pady and Kapica (1955)	Bourdillong slit sampler and McGill GE	$28.3\,l\,min^{-1}$	2 sampling flights Montréal-London
Prospero et al. (2005)	Filter Samples	$10\,l\,min^{-1}$	1996–1997/continuous samplings
Rodríguez-Rajo et al. (2005) *	Hirst-type spore trap (Lanzoni)	$10\,l\,min^{-1}$	whole year/continuous samplings
Sabariego et al. (2000)	Hirst-type spore trap (Burkart)	$10\,l\,min^{-1}$	whole year/continuous samplings
Sakiyan and Inceoglu (2003) †	Hirst-type spore trap (Burkart)	$10\,l\,min^{-1}$	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	$10\,l\,min^{-1}$	Daily average concentrations 1997–1999
Winiwarter et al. (2009)	Data taken from multiple sources	n/a	n/a
Wu et al. (2004)	Hirst-type spore trap (Burkart)	$10\,l\,min^{-1}$	12 2000–04 2001/continuous sampling
Wu et al. (2007)	Portable air samplers for agar plates	$20\,l\,min^{-1}$	03 2003–12 2004, 2 min/sample/2x monthly

* Considered species: *Cladosporium sp.* and *Alternaria sp.*
† Considered species: *Cladosporium sp.* and *Alternaria sp.*
‡ Considered species: *Alternaria sp.*, *Botrytis sp.*, *Cladosporium sp.*, *Didymella sp.*, and *Ganoderma sp.*

would be of help in order to minimize measurement biases and allow for better intercomparability of measurements. The resulting global emission flux of fungal bioaerosol of $1.69 \times 10^{-11}\,kgm^{-2}s^{-1}$ 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. 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.

Table A2. Data used as input for fungal spore flux calculations; average, minimum and maximum number concentrations and number fluxes of fungal spores. The data were always rounded to a whole number. The column CFU (Culture Forming Units) counts denotes if a culture based technique was used for the analysis (yes), if it was a culture-independent technique (no), or if both methods were used.

Source	Ecosystem	Average conc. [m^{-3}]	Min conc. [m^{-3}]	Max. conc. [m^{-3}]	Average flux [$m^{-2}s^{-1}$]	Min flux [$m^{-2}s^{-1}$]	Max flux [$m^{-2}s^{-1}$]	CFU counts
Amato et al. (2005)	Forest	222	53	390	44	11	78	yes
Bauer et al. (2002a)	Forest	2200	340	5000	440	68	1000	no
Bauer et al. (2002a)	Forest	1200	170	3200	240	34	640	no
Bauer et al. (2002a)	Forest	346	49	863	69	10	173	no
Beaumont et al. (1985)	Forest	258	n/a	n/a	52	n/a	n/a	yes
Côté et al. (2008)	Forest	615	492	738	123	98	148	yes
Fisar et al. (1990)	Forest	17	n/a	n/a	3	n/a	n/a	Both methods
Gregory (1967)	Forest	n/a	n/a	43 300	n/a	n/a	8660	no
Gregory (1967)	Forest	5250	n/a	n/a	n/a	n/a	1050	no
Gregory (1967)	Forest	n/a	766	n/a	153	n/a	n/a	no
Kasprzyk and Worek (2006)	Forest	2144	n/a	n/a	429	n/a	n/a	no
Kasprzyk and Worek (2006)	Forest	2183	n/a	n/a	437	n/a	n/a	no
Kasprzyk and Worek (2006)	Forest	2093	n/a	n/a	419	n/a	n/a	no
Kasprzyk and Worek (2006)	Forest	2146	n/a	n/a	429	n/a	n/a	no
Marks et al. (2001)	Forest	105	0	1000	21	0	200	yes
Marks et al. (2001)	Forest	223	0	600	45	0	120	yes
Marks et al. (2001)	Forest	26	0	200	5	0	40	yes
Marks et al. (2001)	Forest	12	0	45	2	0	9	yes
Oliveira et al. (2009)	Forest	531	n/a	8509	106	n/a	1702	no
Rodríguez-Rajo et al. (2005)	Forest	564	n/a	n/a	113	n/a	n/a	no
Winiwarter et al. (2009)	Forest	49	n/a	n/a	10	n/a	n/a	
Elbert et al. (2007)	Tropical forest	12 476	4764	20 188	2495	953	4038	no
Griffin et al. (2001)	Tropical forest	45	n/a	n/a	9	n/a	n/a	no
Griffin et al. (2003)	Tropical forest	0	n/a	n/a	0	n/a	n/a	yes
Griffin et al. (2003)	Tropical forest	57	n/a	n/a	11	n/a	n/a	yes
Griffin et al. (2003)	Tropical forest	9	5	20	2	1	4	yes
Griffin et al. (2003)	Tropical forest	12	8	24	2	2	5	yes
Griffin et al. (2007)	Tropical forest	1702	100	8510	340	20	1702	yes
Lau et al. (2006)	Tropical forest	86	18	341	17	4	68	both methods
Lau et al. (2006)	Tropical forest	72	30	294	14	6	59	both methods
Lau et al. (2006)	Tropical forest	292	7	2386	58	1	477	both methods
Lau et al. (2006)	Tropical forest	247	50	1540	49	10	308	both methods
Prospero et al. (2005)	Tropical forest	92	n/a	n/a	18	n/a	n/a	yes
Prospero et al. (2005)	Tropical forest	213	n/a	n/a	43	n/a	n/a	yes
Pady and Kapica (1955)	Tropical forest	37	6	67	7	1	13	both methods
Pady and Kapica (1955)	Tropical forest	230	170	291	46	24	58	both methods
Pady and Kapica (1955)	Tropical forest	6	6	6	1	1	1	both methods
Pady and Kapica (1955)	Tropical forest	44	39	49	9	8	10	both methods
Pady and Kapica (1955)	Tropical forest	16	n/a	n/a	3	n/a	n/a	both methods
Pady and Kapica (1955)	Tropical forest	31	n/a	n/a	6	n/a	n/a	both methods
Wu et al. (2007)	Tropical forest	2233	n/a	n/a	447	n/a	n/a	yes
Wu et al. (2007)	Tropical forest	2278	n/a	n/a	456	n/a	n/a	yes
Burch and Levetin (2002)	Shrub	50 000	n/a	n/a	10 000	n/a	n/a	no
Herrero et al. (2006)	Shrub	609	n/a	n/a	122	n/a	n/a	no
DiGiorgio et al. (1996)	Shrub	92	n/a	n/a	18	n/a	n/a	no
DiGiorgio et al. (1996)	Shrub	46	n/a	n/a	9	n/a	n/a	no
Griffin et al. (2007)	Shrub	73	31	115	15	6	23	yes
Griffin et al. (2007)	Shrub	25	0	291	5	0	58	yes
Katial et al. (1997)	Shrub	409	n/a	n/a	82	n/a	n/a	no
Pady (1957)	Shrub	24 499	837	48 162	4 900	167	9632	no
Pady (1957)	Shrub	715	170	1261	143	34	252	no
Levetin and Dorsey (2006)	Shrub	24 121	53	48 188	4824	11	9638	yes
Levetin and Dorsey (2006)	Shrub	5459	n/a	64 363	1092	n/a	12 873	yes
Mallo et al. (2010)	Shrub	285	n/a	2000	57	n/a	400	no
Mallo et al. (2010)	Shrub	814	n/a	3488	163	n/a	698	no
Oliveira et al. (2009)	Shrub	934	n/a	8761	187	n/a	1752	no
Rodríguez-Rajo et al. (2005)	Shrub	950	n/a	n/a	190	n/a	n/a	no
Rodríguez-Rajo et al. (2005)	Shrub	979	n/a	n/a	196	n/a	n/a	no
Sabariego et al. (2000)	Shrub	832	n/a	n/a	166	n/a	n/a	no
Sakiyan and Inceoglu (2003)	Shrub	2917	17	5817	583	3	1163	no
Gregory (1952)	Crop	9175	n/a	n/a	1835	n/a	n/a	no

Table A2. Continued.

Source	Ecosystem	Average conc. [m^{-3}]	Min conc. [m^{-3}]	Max. conc. [m^{-3}]	Average flux [$m^{-2}s^{-1}$]	Min flux [$m^{-2}s^{-1}$]	Max flux [$m^{-2}s^{-1}$]	CFU counts
Gregory (1952)	Crop	11900	n/a	n/a	2380	n/a	n/a	no
Gregory (1952)	Crop	6975	n/a	n/a	1395	n/a	n/a	no
Gregory (1952)	Crop	9372	n/a	n/a	1874	n/a	n/a	no
Gregory (1952)	Crop	13970	n/a	n/a	2794	n/a	n/a	no
Gregory (1952)	Crop	9830	n/a	n/a	1966	n/a	n/a	no
Hamilton (1959)	Crop	14 800	n/a	n/a	2960	n/a	n/a	no
Hamilton (1959)	Crop	8200	6400	10 000	1640	1280	2000	no
Wu et al. (2004)	Crop	28684	n/a	n/a	5737	n/a	n/a	no
Griffin et al. (2001)	Grassland	42	n/a	n/a	8	n/a	n/a	no
Griffin et al. (2003)	Grassland	24	n/a	n/a	5	n/a	n/a	yes
Griffin et al. (2003)	Grassland	46	27	57	9	5	11	yes
Griffin et al. (2003)	Grassland	65	48	90	13	10	18	yes
Griffin et al. (2003)	Grassland	11	8	14	2	3	2	yes
Griffin et al. (2007)	Grassland	869	n/a	n/a	174	n/a	n/a	yes
Griffin et al. (2007)	Grassland	215	205	226	43	41	45	yes
Griffin et al. (2007)	Grassland	66	0	703	13	0	141	yes
Griffin et al. (2007)	Grassland	3	0	27	1	0	5	yes
Griffin et al. (2007)	Grassland	1398	336	6992	280	67	1398	yes
Griffin et al. (2007)	Grassland	6078	n/a	n/a	1216	n/a	n/a	yes
Kellogg et al. (2004)	Grassland	225	80	370	45	16	74	yes
Kellogg et al. (2004)	Grassland	65	0	130	13	0	26	yes
Kellogg and Griffin (2006)	Grassland	0	n/a	n/a	0	n/a	n/a	yes (apart from one source)
Kellogg and Griffin (2006)	Grassland	60	n/a	n/a	12	n/a	n/a	yes (apart from one source)
Kellogg and Griffin (2006)	Grassland	6078	n/a	n/a	1216	n/a	n/a	yes (apart from one source)
Kellogg and Griffin (2006)	Grassland	4839	n/a	n/a	968	n/a	n/a	yes (apart from one source)
Prospero et al. (2005)	Grassland	0	n/a	n/a	0	n/a	n/a	yes
Wu et al. (2004)	Grassland	n/a	n/a	29 038	n/a	n/a	5808	no
Pady and Kapica (1955)	Tundra	30	4	57	6	1	11	both methods
Pady and Kapica (1955)	Tundra	87	14	159	17	3	32	both methods
Pady and Kapica (1955)	Tundra	3	2	4	1	0	1	both methods
Pady and Kapica (1955)	Tundra	39	7	71	8	1	14	both methods

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