Atmos. Chem. Phys. Discuss., 6, 11317–11355, 2006
www.atmos-chem-phys-discuss.net/6/11317/2006/

Atmospheric Chemistry and Physics Discussions

Contribution of fungi to primary biogenic aerosols in the atmosphere: active discharge of spores, carbohydrates, and inorganic ions by Asco- and Basidiomycota

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Received: 20 September 2006 – Accepted: 6 November 2006 – Published: 15 November 2006

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Abstract

Spores and related chemical compounds from actively spore-discharging Ascomycota (AAM) and actively spore-discharging Basidiomycota (ABM) are primary biogenic components of air particulate matter (characteristic size range 1–10 μm). Measurement results and budget calculations based on investigations in Amazonia (Balbina, Brazil, July 2001) indicate that the forcible discharge of fungal spores may account for a large proportion of coarse air particulate matter in tropical rainforest regions during the wet season. For the particle diameter range of 1–10 μm, the estimated proportions are ~25% during day-time, ~45% at night, and ~35% on average. For the sugar alcohol, mannitol, the budget calculations indicate that it is suitable for use as a molecular tracer for actively discharged basidiospores (ABS), and that the literature-derived emission ratio of about 5 pg per ABS may be taken as a representative average. ABM emissions may account for most of the atmospheric abundance of mannitol, and can explain the observed diurnal cycle (higher abundance at night). ABM emissions of hexose carbohydrates might also account for a significant proportion of glucose and fructose in air particulate matter, but the literature-derived ratios are not consistent with the observed diurnal cycle (lower abundance at night). AAM emissions appear to account for a large proportion of potassium in air particulate matter over tropical rainforest regions during the wet season, and they can also explain the observed diurnal cycle (higher abundance at night). The results of our investigations and budget calculations for tropical rainforest aerosols are consistent with measurements performed at other locations.

Based on the average abundance of mannitol in particulate matter, which is consistent with the above emission ratio and the observed abundance of ABS, we have also calculated a value of ~17 Tg yr^{-1} as a first estimate for the global average emission rate of ABS over land surfaces. Comparisons with estimated rates of emission and formation of other major types of organic aerosol (~47 Tg yr^{-1} of anthropogenic primary organic aerosol; 12–70 Tg yr^{-1} of secondary organic aerosol) indicate that emissions from actively spore-discharging fungi should be taken into account as a significant

source of organic aerosol. Their effects might be particularly important in tropical regions, where both physicochemical processes in the atmosphere and biological activity at the Earth's surface are particularly intense, and where the abundance of fungal spores and related chemical compounds are typically higher than in extratropical regions.

1 Introduction

Biogenic aerosols are ubiquitous in the Earth's atmosphere and they influence atmospheric chemistry and physics, the biosphere, climate, and public health. They play an important role in the spread of biological organisms and reproductive materials, and they can cause or enhance human, animal, and plant diseases. Moreover, they influence the Earth's energy budget by scattering and absorbing radiation, and they can initiate the formation of clouds and precipitation as cloud condensation and ice nuclei (Dingle, 1966; Schnell and Vali, 1972; Cox and Wathes, 1995; Andreae and Crutzen, 1997; Hamilton and Lenton, 1998; Andreae et al., 2002; Taylor and Jonsson, 2004; Jaenicke, 2005; Lohmann and Feichter, 2005; Pöschl, 2005; Dusek et al., 2006; McFiggans et al., 2006; Sun and Ariya, 2006; and references therein). The composition, abundance, and origin of biogenic aerosol particles and components are, however, still poorly understood and quantified.

Primary biogenic aerosol (PBA) particles and components are emitted directly from the biosphere to the atmosphere. Examples of PBA particles are pollen, bacteria, fungal and fern spores, viruses, and fragments of animals and plants (Simoneit and Mazurek, 1982; Matthias-Maser and Jaenicke, 1992; Artaxo and Hansson, 1995; Bauer et al., 2005). PBA components comprise the non- or semi-volatile chemical substances contained in PBA particles as well as the biogenic substances contained in other types of aerosol particles such as soil dust, sea spray, etc. (Fuzzi et al., 2006a).

The occurrence and dispersion of microorganisms and spores in the air has been discussed and investigated very early in the history of aerosol science (Ehrenberg, 1830; Pasteur, 1860a, 1860b). Since then, aircraft, balloon, and rocket measurements have shown that PBA particles are not only ubiquitous over land and oceans but also transported to high altitudes (up to 80 km) and over long distances (Scheppergrell, 1924; Proctor, 1934; Meier, 1935; Rogers and Meier, 1936; Pady et al., 1950; Gregory, 1978; Imshenetsky et al., 1978; Watson and DeSousa, 1983; Griffin et al., 2001; McCarthy, 2001; Brown and Hovmoller, 2002; Yeo and Kim, 2002; Wainwright et al., 2003; Prospero et al., 2005).

Pollen grains, fern spores, large fungal spores, and other large PBA particles typically belong to the coarse fraction of air particulate matter, with aerodynamic diameters up to one hundred micrometers. PBA particles and components are, however, also found in intermediate and fine fractions of air particulate matter, with aerodynamic diameters less than 10 μm (PM10), 2.5 μm (PM2.5), and 1 μm (PM1), respectively: most fungal spores, small fragments and excretions of plants and animals, bacteria, viruses (Górny et al., 2002; Taylor et al., 2004); carbohydrates, proteins, waxes, ions, etc. are in this size range (Fish, 1972; Beauford et al., 1975; Miguel et al., 1999; Zhang and Anastasio, 2003; Franze et al., 2005; Pöschl, 2005). So far, however, the biological, chemical, and physical effects and mechanisms involved in the emission and dispersion of PBA particles and components have received little attention in biogeoscience and atmospheric research.

Here, we present and discuss evidence that the forcible discharge of spores from certain fungi is accompanied by the emission of aqueous droplets containing carbohydrates and inorganic ions. This is likely to account for a large proportion of these compounds in air particulate matter, especially in pristine tropical rainforests. We summarize the information available from earlier scientific publications and present new measurement data and budget calculations for aerosol samples from Amazonia. Furthermore, we derive a first estimate for the global emission rate of actively discharged basidiospores.

2 Active discharge of fungal spores by Ascomycota and Basidiomycota

The number of different fungal species in the biosphere is assumed to be in the range of 1–1.5 million, but only about 40 000 are well-characterized (Rossman, 1994). They are usually grouped into the three divisions (phyla) of Ascomycota, Basidiomycota, and Zygomycota. A fourth category is called "mitosporic fungi" (formerly known as Chytridomycota, Deuteromycetes or "Fungi Imperfecti") (Ribes et al., 2000).

Fungi exist in terrestrial and aquatic habitats, and their reproduction proceeds via budding or sporulation, using a variety of dispersal mechanisms (Buller, 1909–1950; Ingold, 1971, 1999). Here we concentrate on those species of Ascomycota and Basidiomycota that actively discharge their spores into the air, which we designate as "actively spore-discharging Ascomycota" (AAM) and "actively spore-discharging Basidiomycota" (ABM).

2.1 Actively spore-discharging Ascomycota (AAM)

AAM exist as saprophytes on dead biomass as well as endophytes or parasites in/on living organisms. In combination with algae, they form lichens which live as epiphyles on plants or on other surfaces, such as rocks, house walls etc. They are found in most regions and climate zones of the world.

The spores of AAM, which we designate as actively discharged ascospores (AAS), are typically 2–20 μm in diameter (Buller, 1909; Ingold, 2001b) and mature within apothecia. These are composed of small sacks (asci) filled with epiplasmic fluids, and they contain a mix of organic and inorganic solutes. For example, a mature ascus of *Giberella zeae* holds a liquid volume of $\sim 7\times10^{-15}$ m^3 with mannitol ($4.7\pm2.2\times10^{-12}$ g), potassium (4.6×10^{-11} g), and chloride (1.4×10^{-11} g) as the main solutes (Trail et al., 2005). Glycerol and proline (37 ± 6 and 8 ± 3 mmol/L, respectively) were found in the ascus sap of *Ascobolus immersus* (Fischer et al., 2004). To our knowledge, other data on the chemical composition of ascus sap are not available.

The asci are pressurized osmotically and, upon discharge, spores and droplets of epiplasmic fluid are vigorously ejected through a narrow aperture at the tip of the bursting asci (Buller, 1909; Ingold, 2001a; Trail et al., 2002). The size and number of the ejected aqueous droplets are similar to the size and number of spores (twice as many droplets in the case of *Giberella zeae*, Trail et al., 2002). The discharge distance ranges from about one to several hundred millimeters in still air (Buller, 1909; Ingold, 1971; Meredith, 1973).

Raynal (1990) found that individual apothecia of *Sclerotinia trifoliorum* ejected up to 4.7×10^6 AAS over their entire life cycle. Ingold (1971) reported that individual apothecia of *Cookeina sulcipes* can discharge $3–24\times10^6$ AAS, and Hong and Michailides (1998) determined a release of $2–37\times10^6$ AAS per AAM fruiting body of *Monilinia fructicola*. Venette (1998) reported that a single apothecium of *Sclerotinia sclerotiorum* can discharge $2–30\times10^6$ AAS over a period of several days and estimated a potential spore load of $0.2–3\times10^{12}$ AAS for this fungus per ha of grain field (Table 1).

2.2 Actively spore-discharging Basidiomycota (ABM)

ABM comprise mushrooms, bracket and jelly fungi, smut and rust fungi, as well as basidiomyceteous yeasts (mirror yeasts). The rusts have a complex life cycle with several stages, and during one of these emit actively discharged basidiospores (ABS), which are also called ballistospores. Mirror yeasts are dimorphic fungi; they can grow in a hyphal form like yeasts, but can also discharge ABS. Most of the other ABM emit ABS from basidia (little pedestals) aligned along gills, in tubes, or on the surface of their fruiting bodies.

The diameter of ABS typically range from 2 to 10 μm. (Ingold, 2001b). Their active discharge was noted in the 19th century, but only recently was the discharge mechanism resolved and termed "surface tension catapult" (Turner and Webster, 1991; Pringle et al., 2005). It involves an aqueous droplet near the basal end of the spore called the "Buller's drop" (Buller, 1915, 1922; Buller and Vanterpool, 1925), and a thin liquid film on the distal end of the spore. At high relative humidity they both grow by hygroscopic uptake of water vapor. Upon reaching a size comparable to the spore,

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the Buller's drop and the liquid film merge, and the generated momentum propels the spore, enveloped by the liquid, away from the basidium – typically over distances of 0.1–1.5 mm (Webster et al., 1989; Turner and Webster, 1995; Ingold, 1999; Pringle et al., 2005).

The solutes found in Buller's drops of the basidiomycetous yeast *Itersonilia perplexans* are mainly hexoses and mannitol (3.8 and 5.3 pg per spore, respectively) plus smaller (but not quantified) quantities of inorganic ions like phosphate, sodium and potassium (Webster et al., 1995). To our knowledge, other data on the chemical composition of the Buller's drop are not available.

Buller (1909) reported that a single fruiting body of a mushroom (basidiocarp) can discharge as many as 4–10×10^7 ABS per hour (*Psalliota campestris* and *Coprinus comatus*), 6.8×10^8 ABS per week (*Daedalea confragosa*), or 1–10×10^{10} ABS per year (*Polyporus squamosus*), respectively (Table 1). Meredith (1973) reported discharge rates of 3×10^{10} ABS per day over periods up to 6 months for artist's conk (*Ganoderma applanatum*).

Besides AAM and ABM, other fungal species also actively discharge their propagating units with liquid jets or droplets, e.g., *Basidiobolus*, *Conidiobolus*, *Entomophtora*, *Pilobolus* and *Sphaerobolus stellatus* (Buller, 1909; Couch, 1939; Page, 1964; Ribes et al., 2000). The chemical composition of these liquids is, however, not known, and thus not included in the present study.

3 Abundance of fungal spores and related chemical components in air particulate matter

3.1 Actively discharged ascospores (AAS) and basidiospores (ABS)

The abundance of fungal spores in the air is highly variable, and is dependent upon location, season, time of day, and weather. Air masses with low concentrations of spores can be intercepted by plumes with very high concentrations (Chatterjee and

Hargreave, 1974; Burch and Levetin, 2002). Specific information on the atmospheric abundance of AAS and ABS is very limited. In a comprehensive literature search we found some data from ground based aerosol investigations, but none from airborne sampling.

Table 2 summarizes ambient concentrations of AAS (a) and ABS (b) reported in earlier studies, and the results of our microscopic investigations of aerosol filter samples collected in the tropical rainforest of Amazonia. Overall, the concentrations range from zero to $\sim 10^4\,m^{-3}$, with exceptional maximum values up to $\sim 10^6\,m^{-3}$ observed for AAS during the harvesting of barley. Most of the concentrations reported for AAS and ABS, including the few data available from tropical regions (Brazil, Mexico, Taiwan), range between $10^3\,m^{-3}$ and $10^4\,m^{-3}$.

These data for AAS and ABS are consistent with recent studies investigating total concentrations of fungal spores in alpine air ($\sim 10^3\,m^{-3}$; Mt. Rax, Austria) and urban air (8–26 $10^3\,m^{-3}$; Vienna, Austria), corresponding to 2–6% of the organic carbon fraction and up to 1.3% of the total mass of air particulate matter (Bauer et al., 2002, 2005). In rural air over an agricultural region, Burch and Levetin (2002) recorded concentrations of total fungal spores in the range of $2–17\times 10^4\,m^{-3}$ (Bixby/Tulsa, USA). They also reported that passively discharged fungal spores were generally enhanced during warm, dry weather conditions, whereas AAS and ABS tended to be more concentrated during wet or humid conditions, such as those at night and in the early morning. Precipitation appeared to be required for the release of spores from many AAM, and AAS concentrations usually increased during and after rainstorms. The release and resultant airborne concentrations of ABS, on the other hand, appeared to be more directly correlated with relative humidity rather than precipitation (Ingold, 1971; Chatterjee and Hargreave, 1974; Burch and Levetin, 2002).

Air samples used in our investigations were collected at the beginning of the dry season at Balbina, Amazonia, Brazil, (1°55′ S, 59°24′ W, 174 m above sea level) on a pasture site adjacent to pristine tropical rainforest. Samples for microscopic examination were taken with a rotating impactor and with an isokinetic 2-stage jet impactor positioned 2 m above the ground. Air samples for the determination of inorganic ions in fine particulate matter (≤2 μm) and coarse particles (2–10 μm) were taken with two-stage stacked filter units (SFU). Sugars and sugar alcohols were determined in aerosol particle samples collected with a dichotomous high-volume (HiVol) sampler: fine (≤2.5 μm) and coarse (≥2.5 μm). Both the SFU and the HiVol samplers were positioned 4 m above the ground (Graham et al., 2003a; Graham et al., 2003b; Moura et al., 2004).

AAS and ABS were determined by detailed microscopic investigation of two exemplary samples collected with the jet impactor on 22 July 2001 (local time of sampling: 09:10–09:48 and 23:55–01:05). The samples were mounted and directly observed with a Nikon 80i light microscope at up to 1500x magnification. Fungal spore types were identified based on their morphology in 200 fields of view for each sample. Counts were expressed per cubic meter of air sampled.

Fungal spores (2–20 μm) were generally most abundant in night-time samples when the relative humidity was close to 100%, whereas the concentration of larger fern spores and pollen was typically higher in day-time samples (Graham et al., 2003a). The night-time concentrations were ∼7400 m^{-3} for AAS and ∼12 800 m^{-3} for ABS (∼3600 m^{-3} from rust fungi and ∼9150 m^{-3} from smut fungi); the day-time concentrations were ∼3000 m^{-3} for AAS and ∼1800 m^{-3} for ABS (almost exclusively from rust fungi). The results are consistent with the general trends and concentrations of AAS, ABS, and total fungal spores observed in earlier investigations (as outlined above) and in a recent study of colony-forming spores sampled from a tropical rainforest in Australia (Gilbert and Reynolds, 2005).

3.2 Carbohydrates: mannitol, glucose, and fructose

Table 3 gives an overview of the concentrations reported for the sugar alcohol mannitol ($C_6H_{14}O_6$) in atmospheric aerosols. At extratropical locations, the average concentrations of mannitol were 1–11 ng m^{-3} for particles ≤2.5 μm and 0–220 ng m^{-3} for particles ≥2.5 μm. In aerosol samples from Amazonia and Rondônia (Brazil), average mannitol concentrations were 2–3 times higher than at extratropical locations: 8–26 ng m^{-3}

for particles ≤2.5 µm, and 29–112 ng m^{-3} for particles ≥2.5 µm. Investigations with separate day-time and night-time samples of particles ≥2.5 µm showed that the night-time concentrations of mannitol were higher by factors of 2–3 (Graham et al., 2002, 2003b; Claeys et al., 2004). Recent investigations with an 11-stage MOUDI aerosol impactor showed that the mass size distribution of mannitol in tropical rainforest aerosols (Rondônia, Brazil) exhibited a maximum at particle diameters around 5 µm. The maximum was particularly pronounced (up to three orders of magnitude higher than the lowest values of the size distribution function) during nights of the dry season and throughout the transition and wet seasons (Decesari et al., 2006; Fuzzi et al., 2006b). In the wet season the total aerosol mass size distribution function was also dominated by a pronounced maximum at particle diameters around 5 µm (Fuzzi et al., 2006b).

Table 4 gives an overview of the atmospheric concentrations observed for the hexose sugars, glucose and fructose ($C_6H_{12}O_6$). In contrast to mannitol, the glucose and fructose concentrations determined in samples of air particulate matter from Amazonia and Rondônia (Brazil), were not higher than at extratropical locations: 1–49 ng m^{-3} (≤2.5 µm) and 3–146 ng m^{-3} (≥2.5 µm) at tropical locations; 10–15 ng m^{-3} (≤2.5 µm) and 1–270 ng m^{-3} (≥2.5 µm) at extratropical locations. Moreover, studies with separate day-time and night-time sampling at tropical sites showed a diurnal cycle opposite to that of mannitol: glucose and fructose concentrations were strongly enhanced during day-time (up to 50 times higher than at night) (Graham et al., 2003b).

3.3 Inorganic Ions: potassium and chloride

Tables 5 and 6 give an overview of potassium and chloride ion concentrations in atmospheric aerosols observed during the wet season at various locations in Amazonia. The concentrations of potassium were typically in the range of 24–220 ng m^{-3} for particles ≤2 µm and 14–270 ng m^{-3} for particles in the size range of 1–15 µm, respectively, and night-time concentrations generally exceeded day-time concentrations (Graham et al., 2003a; Fuzzi et al., 2006b). The chloride concentrations were in the range of

5–65 ng m^{-3} for particles ≤2 μm and 8–155 ng m^{-3} for particles with diameters of 2–15 μm, respectively.

3.4 Total air particulate matter

Table 7 lists total particle mass concentrations recorded during the wet season at various locations in Amazonia. Long-term average values for the particle size range of 2–10 μm were typically 5–16 μg m^{-3} (Artaxo et al., 1990; Formenti et al., 2001; Guyon et al., 2003). Studies with separate day- and night-time sampling showed that particle mass concentrations were 2–4 times higher at night (Graham et al., 2003a; Fuzzi et al., 2006b).

4 Contribution of AAM and ABM emissions to the mass and chemical composition of Amazonian rainforest aerosols

To calculate an estimate of the relative contribution of fungal emissions to the chemical composition of coarse air particulate matter (particle diameters 1–2 μm to 10–15 μm) in the tropical rainforest of Amazonia during the wet season, we used the parameters listed in Table 8, which have been derived from the literature (Webster et al., 1995; Trail et al., 2005). For the average mass of AAS we assumed a value of 200 pg for AAS, corresponding to a volume equivalent diameter of ~7 μm and density of ~1 g cm^{-3} (Trail et al., 2005). For ABS we assumed an average mass of 65 pg, corresponding to a volume equivalent diameter of ~5 μm and density of ~1 g cm^{-3} (Buller, 1909; Ingold, 1971; Lin and Li, 1996; Ingold, 2001b; Wu et al., 2004) and consistent with the maximum of mannitol and PM size distributions observed in tropical rainforest aerosols during the wet season (Fuzzi et al., 2006b). This is a lower estimate compared to the 840 pg per ABS of *I. perplexans* reported by Turner and Webster (1991), which would correspond to a volume equivalent diameter of ~12 μm at ~1 g cm^{-3}. For AAS, the number of spores per ascus can vary over a range of about 1–100. Nevertheless, an average number of 8 spores per ascus has been determined for the majority of AAM used in our calculations (Ingold, 1971).

By multiplication of the parameters outlined above with the measured number concentrations of AAS and ABS, we obtained the mass concentration estimates listed in Table 9 and illustrated in Figs. 1–4.

For mannitol (Fig. 1), the estimated fungal emissions are dominated by ABS and account for 100% of the night-time, 35% of the day-time, and 80% of the average concentrations, which have been determined in two independent measurements at the same location and period of time (Balbina: 19–28 July 2001, (Graham et al., 2003b); 25–28 July 2001, (Claeys et al., 2004); particle diameters ≥2.5 μm).

For the hexoses (Fig. 2), the fungal emission estimate (related to ABS only) exceeds the measured night-time concentrations of glucose and fructose by a factor of 10. During day-time the estimated fungal emissions would account for only ∼10%, and averaged over 24 hours they would account for ∼60% of the observed concentrations.

For potassium (Fig. 3), the estimated fungal emissions (related to AAS only) account for ∼60% of the average concentration measured at the same location and period of time (Balbina: 16–28 July 2001, (Graham et al., 2003a); particle diameters 2–10 μm; separate day- and night-time values not available). Compared to measurement data from a different place and time during the wet season in Amazonia (FNS: Fazenda Nossa Senhora Aparecida, near Ouro Preto do Oeste, Rondônia) (Fuzzi et al., 2006b), the day- and night-time estimates would account for practically all of the potassium in the investigated aerosol particle size range (1–10 μm) and are consistent with the observed diurnal cycle.

For chloride (Tables 6 and 9), the estimated fungal emissions (related to AAS only) account for ∼15% of the average concentration measured at the same location and period of time (Balbina: 16–28 July 2001, (Graham et al., 2003a); particle diameters 2–10 μm; separate day- and night-time values not available).

For total mass of particulate matter (Fig. 4), the estimated emissions by actively spore discharging fungi are dominated by the spores rather than the solutes (solute

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mass fraction only 5–10%) and account for ∼45% of the night-time, ∼25% of the day-time, and ∼35% of the average concentrations measured at the same location and period of time (Balbina: 22–25 July 2001, (Graham et al., 2003a); particle diameters 2–10 μm). Compared to measurement data from FNS (Fuzzi et al., 2006b), the estimated proportion of fungal emissions in particles sized 1–10 μm in diameter would be slightly lower at night, higher during the day, and similar on average.

5 Global emission rate of ABS

As outlined above (Sect. 3.1, Table 2), the knowledge about the abundance and activity of fungi in the global biosphere is very limited, and regional or global estimates for the emission rate and flux of actively-discharged fungal spores are not yet available in the literature.

Here, we calculate a first estimate for the global average emission rate of ABS over land surfaces based on the following first-order approximations and assumptions:

1) The abundance of mannitol in the atmosphere is assumed to be dominated by emissions from ABM, which is supported by the literature data and results outlined above (Table 2: similar abundance of AAS and ABS; Table 8: higher amount of mannitol emitted with one ABS per Buller's drop compared to eight AAS per ascus; Table 9 and Fig. 1: consistency of exemplary calculations).

2) The literature-derived value of 5 pg mannitol emitted per ABS (Table 8) is assumed to be representative for ABM, which is supported by the results outlined above (Table 9 and Fig. 1: consistency of exemplary calculations).

3) The average value of mannitol concentrations reported for PM with particle diameters up to 10 μm or more at extratropical measurement locations (25 ng m^{-3}, Table 3, lines 9–15) is assumed to be representative for a well-mixed continental boundary layer (CBL) with an average height of 1 km (Seinfeld and Pandis, 1998). The following evidence supports these assumptions as conservative: significantly higher mannitol concentrations reported from tropical regions (Table 3); significantly higher and well-mixed

day-time CBLs in tropical regions (Graham et al., 2003b); observation of elevated spore concentrations in the upper part of the CBL (Meier and Artschwager, 1938; Linskens and Jorde, 1986).

4) The average size and atmospheric residence time of ABS are assumed to be on the order of 5 μm and 1 day, respectively, which is supported by the literature data and results outlined above (Table 9 and Fig. 4: consistency of exemplary calculations) and by the basic concepts of atmospheric aerosol cycling (rapid sedimentation and wet deposition of coarse particles).

Dividing the average mannitol concentration of 25 ng m^{-3} by 5 pg (amount of mannitol emitted per ABS) we obtain a value of 5×10^3 m^{-3} as a first-order estimate for the global average number concentration of ABS in the continental boundary layer, which is consistent with the observations summarized in Table 2b and discussed in Sect. 3.1. Multiplication with an average spore mass of 65 pg yields a value of an average contribution of 0.3 μg m^{-3} to the concentration of air particulate matter, which is also consistent with the observations reported in Sect. 3.1. As demonstrated above, the total mass concentration of actively discharged spores and related substances observed in tropical rainforest regions during the wet season are significantly higher, supporting the above values as conservative estimates.

Multiplication of the average number concentration with an average CBL height of 1000 m and division by an average residence time of 1 day yields an estimate of $\sim5\times60$ m^{-2} s^{-1} for the globally averaged land surface emission flux of ABS. By multiplication with an average spore mass of 65 pg, the global land surface area of 1.5×10^{14} m^2 and the duration of one year we obtain an estimate of ~17 Tg yr^{-1} for the global emission rate of ABS.

For comparison: current estimates of the rates of emission and formation of other types of air particulate matter are ~47 Tg yr^{-1} for anthropogenic primary organic aerosols (POA: 35 Tg yr^{-1} from vegetation fires, 9 Tg yr^{-1} from biofuel combustion, 3 Tg yr^{-1} from fossil fuel combustion) and 12–70 Tg yr^{-1} for secondary organic aerosols (SOA: mostly from oxidation of biogenic terpenes; Kanakidou et al., 2005).

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6 Summary and conclusions

In this study we have gathered and summarized qualitative and quantitative information on the atmospheric abundance and emission of spores and related chemical compounds from AAM and ABM. These primary biogenic components of coarse air particulate matter (characteristic size range 1–10 μm) may influence the formation of clouds and precipitation as cloud condensation and ice nuclei, and they affect the spread and reproduction of organisms in the biosphere. The effects of fungal emissions might be particularly important in tropical regions where both physicochemical processes in the atmosphere and biological activity at the Earth's surface are particularly intense.

Measurements and budget calculations based on our investigations in Amazonia (Balbina, Brazil, July 2001) indicate that the forcible discharge of fungal spores may account for a large proportion of coarse air particulate matter in tropical rainforest regions during the wet season. For the particle diameter range of 1–10 μm the estimated proportions are ~25% during day-time, ~45% at night, and ~35% on average. For the sugar alcohol mannitol, the budget calculations indicate that it may be used as a molecular tracer for ABS, that the literature-derived emission ratio of about 5 pg per ABS may be taken as a representative average, and that the ABM emissions may account for most of its atmospheric abundance and can explain the observed diurnal cycle (higher abundance at night). ABM emissions of hexose carbohydrates might also account for a significant proportion of glucose and fructose in aerosols, but the literature-derived emission factors are not consistent with the observed diurnal cycle (lower abundance at night). AAM emissions appear to account for a large proportion of potassium in aerosols over tropical rainforest regions during the wet season, and they can also explain the observed diurnal cycle (higher abundance at night). The results of our investigations and budget calculations for tropical rainforest aerosols are consistent with measurements performed at other locations in Amazonia.

Based on the average abundance of mannitol in air particulate matter, which is consistent with the above emission ratio and observed abundance of ABS, we have also

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calculated a value of $\sim$17 Tg yr^{-1} as a first estimate for the global average emission rate of ABS over land surfaces. Comparison with estimated rates of emission and formation of other major types of organic air particulate matter ($\sim$47 Tg yr^{-1} of anthropogenic POA; 12–70 Tg yr^{-1} of SOA) indicates that the emissions from actively spore-discharging fungi should be taken into account as a significant source of organic air particulate matter. Their effects might be particularly important in tropical regions, where both physicochemical processes in the atmosphere and biological activity at the Earth's surface are particularly intense, and where the abundance of fungal spores and related chemical compounds are typically higher than in extratropical regions.

For further insight and understanding of seasonal and regional variations, vertical profiles, and long-range transport of fungal spores and related aerosol components, additional ground-based and airborne measurements of these species will be required. Moreover, a reliable assessment of the overall role of bioaerosols in the climate system and of the relative importance of fungal emissions will require similar investigations for other abundant primary biogenic aerosol particles such as pollen and bacteria.

Acknowledgements. This study is based on results from the Large-Scale Atmosphere-Biosphere Experiment in Amazonia (LBA) and was funded by the Max Planck Society. P. Taylor acknowledges financial support by a grant from the Southern California Environmental Health Sciences Center (NIEHS 5P30 ES07048), a Boswell Fellowship from Caltech and the Huntington Medical Research Institute. P. Taylor also thanks R. C. Flagan, Caltech, and E. Newbigin, University of Melbourne. Special thanks are due to C. Morris for helpful comments, and to T. W. Andreae for help with the preparation of the manuscript.

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Table 1. Active discharge of spores by Ascomycota (AAM) and Basidiomycota (ABM).

Amount	Unit	Species	References
		Ascomycota	
$2–37\times10^6$	per apothecium	*Monilinia fructicola*	(Hong and Michailides, 1998)
$3–24\times10^6$	per apothecium	*Cookeina sulcipes*	(Ingold, 1971)
$0.2–4.7\times10^6$	per apothecium	*Sclerotinia trifoliorum*	(Raynal, 1990)
$2–30\times10^6$	per apothecium	*Sclerotinia sclerotiorum*	(Venette, 1998)
$0.2–3\times10^{12}$	per ha	*Sclerotinia sclerotiorum*	(Venette, 1998)
		Basidiomycota	
4×10^7	per fruiting body and hour	*Psalliota campestris*	(Buller, 1909)
1×10^8	per fruiting body and hour	*Coprinus comatus*	(Buller, 1909)
$1–10\times10^{10}$	per fruiting body and year	*Polyporus squamosus*	(Buller, 1909)
6.8×10^8	per fruiting body and week	*Daedalea confragosa*	(Buller, 1909)
3×10^{10}	per fruiting body and day	*Ganoderma applanatum*	(Meredith, 1973)

Table 2. Number concentrations of actively discharged ascospores, AAS (a), and actively discharged basidiospores, ABS (b), observed in ambient air.

AAS Concentration (10^3 m^{-3})	Species	Location and Time	References
(a)			
0–39	*Monilinia fructicola*	Hastings, NZ (August–September)	(Tate and Wood, 2000) [a]
0.1–9.3	*Gibberella zeae*	Quebec, Canada (July)	(Paulitz, 1996) [b]
0–15.2	*Gibberella zeae*	Manitoba, Canada (July–August)	(Inch et al., 2005)
0.01–1.5	*Gibberella zeae*	Ottawa, Canada (June–July)	(Fernando et al., 2000)
≤2.0	*Leptosphaeria*	Ontario, Canada (May–October)	(Li and Kendrick, 1995)
0.04–2.1	*Venturia inaequalis*	Ontario, Canada (April–May)	(Warner and Braun, 1992)
7.4	*Sclerotinia sclerotiorum*	USA	(Venette, 1998)
0.1–1	*Gibberella zeae*	Pennsylvania, USA (April–October)	Ayers et al., 1975, cited by Paulitz (1996)
≤2.5	various	Rochester, USA (April–September)	(Decco et al., 1998)
0.5–2.2	various	Oklahoma, USA (September)	(Sterling et al., 1999)
0.1–45	various	Oklahoma, USA (May)	(Troutt and Levetin, 2001)
0.1–15.6	*Venturia inaequalis*	Southeastern Norway (April–June)	(Stensvand et al., 1998)
≤0.6	various	Derby, UK (January–December)	(Newson et al., 2000)
≤2000	*Didymella exitialis*	Blandford, UK (August)	(Frankland and Gregory, 1973)
≤4.4	*Didymella exitialis*	Edinburgh, UK (July–October)	(Richardson, 1996)
0.03–5.9	*Venturia inaequalis*	Northern Italy (March–April)	(Rossi et al., 2003)
0–14.3	*Pleospora allii*	Cordoba, Spain (March–May)	(Prados-Ligeroet al., 2003)
≤90	*Phyllachora maydis*	Poza Rica, Mexico (February–April)	(Hock et al., 1995) [b]
2.5–3.3	various	Taiwan (September–April)	(Wu et al., 2004)
7.4	various	Balbina, Brazil (July)	this work
(b)			
≤2.8	various	Ontario, Canada (May–October)	(Li and Kendrick, 1995)
0–0.05	Rusts	Rochester, USA (April–September)	(Decco et al., 1998)
0–0.25	Smuts	Rochester, USA (April–September)	(Decco et al., 1998)
0–0.5	various	Rochester, USA (April–September)	(Decco et al., 1998)
0.1–5.5	various	Oklahoma, USA (May)	(Troutt and Levetin, 2001)
0.6–1.6	various	Oklahoma, USA (September)	(Sterling et al., 1999)
≤ 3	various	Oklahoma, USA (May–November)	(Levetin, 1990)
≤30	various	Harpenden, UK (July–September)	(Gregory and Hirst, 1952)
≤10	various	Cardiff, UK (June–October)	(Adams et al., 1968)
5.4	various	Derby, UK (January–December)	(Newson et al., 2000)
≤3	various	Bern, Switzerland (June–October)	(Helbling et al., 2002)
0.5–6	various	Saudi Arabia (January–December)	(Hasnain et al., 2005)
0–0.15	Rusts	Saudi Arabia (January–December)	(Hasnain et al., 2005)
0.5–4	Smuts	Saudi Arabia (January–December)	(Hasnain et al., 2005)
≤4.6	various	Mexico City, Mexico (January–November)	(Calderon et al., 1995)
1.3–2.9	various	Taiwan (April–September)	(Wu et al., 2004)
0.06	Rusts	Taiwan (September–April)	(Wu et al., 2004)
0.5	Smuts	Taiwan (September–April)	(Wu et al., 2004)
3.6	Rusts	Balbina, Brazil (July)	this work
9.2	Smuts	Balbina, Brazil (July)	this work

[a] original data normalized by time; [b] data from infested plots.

Table 3. Mannitol mass concentrations in ambient air observed for different ranges of aerosol particle size (aerodynamic diameter), sampling locations, and seasons.

Average Concentration ($ng\,m^{-3}$)	Concentration Range ($ng\,m^{-3}$)	Particle Diameter (μm)	Location and Time	References
			Extratropical	
0.7	0.5–1.3	≤1	Hyytiälä, Finland (fall)	(Kourtchevet al., 2005a)
1.9	1.2–3.4	≤1	Hyytiälä, Finland (summer)	(Kourtchev et al., 2005a)
10.1	1.3–29	≤2.5	K-puszta, Hungary (summer, day)	(Ion et al., 2005)
2.3	0.6–12	≤2.5	K-puszta, Hungary (summer, night)	(Ion et al., 2005)
10.7	5.4–26	≤2.5	Jülich, Germany (summer)	(Kourtchev et al., 2005b)
–	3–66	≤7	Kobe City, Japan	(Suzuki et al., 2001)
–	1.6–23	≤10	Melpitz, Germany (spring)	(Carvalho et al., 2003)
–	0.5–88	≤10	Hyytiälä, Finland (summer)	(Carvalho et al., 2003)
4.3	0–10	≤10	Birkenes, Norway	(Yttri et al., 2005)
8.1	1.1–19	≤10	Oslo, Norway	(Yttri et al., 2005)
20.0	9–30	≤10	Oslo, Norway	(Yttri et al., 2005)
26.0	7.8–70	≤10	Ghent, Belgium (winter)	(Pashynska et al., 2002)
97.0	31–220	≤10	Ghent, Belgium (summer)	(Pashynska et al., 2002)
4.2	0.9–14	0.06–16	Elverum, Norway (winter)	(Yttri et al., 2005)
18.0	12–24	0.06–16	Elverum, Norway (summer)	(Yttri et al., 2005)
			Tropical (Brazil), Wet Season	
22.3	4.7–56	≤2.5	Reserva Biologica Jarú, Rondônia (1999)	(Graham et al., 2002)
26.3	9.9–50	≤2.5	FNS, Rondônia (1999)	(Graham et al., 2002)
20.8	11–31	≤2.5	FNS, Rondônia (2002)	(Decesari et al., 2006)
9.4	–	≤2.5	Balbina, Amazonas (day) (2001)	(Claeys et al., 2004)
8.4	–	≤2.5	Balbina, Amazonas (night) (2001)	(Claeys et al., 2004)
15.2 [a]	9.6–24	≤2.5	Balbina, Amazonas (day) (2001)	(Graham et al., 2003b)
13.0	–	≤2.5	Balbina, Amazonas (day) (2001)	(Graham et al., 2003b)
17.0	–	≤2.5	Balbina, Amazonas (night) (2001)	(Graham et al., 2003b)
112.0	58–330	TSP [b]	Balbina, Amazonas (1998)	(Claeys et al., 2004)
32.0	–	≥2.5	Balbina, Amazonas (day) (2001)	(Claeys et al., 2004)
68.0	–	≥2.5	Balbina, Amazonas (night) (2001)	(Claeys et al., 2004)
53.3 [a]	24–102	≥2.5	Balbina, Amazonas (day) (2001)	(Graham et al., 2003b)
29.0	–	≥2.5	Balbina, Amazonas (day) (2001)	(Graham et al., 2003b)
78.0	–	≥2.5	Balbina, Amazonas (night) (2001)	(Graham et al., 2003b)

[(a)] average of campaign (19–28 July 2001); [(b)] TSP: total suspended particles.

Table 4. Hexose (glucose, Glc; fructose, Fru) mass concentrations in ambient air observed for different ranges of aerosol particle size (aerodynamic diameter), sampling locations, and seasons.

Substance	Average Concentration ($ng\,m^{-3}$)	Concentration Range ($ng\,m^{-3}$)	Particle Diameter (μm)	Location and Time	References
				Extratropical	
Glc	15	11–26	≤2.5	Jülich, Germany (summer)	(Kourtchev et al., 2005b)
Glc	–	1.3–41	≤10	Hyytiälä, Finland (summer)	(Carvalho et al., 2003)
Glc	3.7	0.9–7.2	≤10	Birkenes, Norway	(Yttri et al., 2005)
Glc	47	8.4–93	≤10	Oslo, Norway	(Yttri et al., 2005)
Glc	22	5.4–32	≤10	Elverum, Norway (winter)	(Yttri et al., 2005)
Glc	19	10–34	≤10	Elverum, Norway (summer)	(Yttri et al., 2005)
Glc	–	28–180	≤10	Melpitz, Germany (spring)	(Carvalho et al., 2003)
Glc	73	30–153	≤10	Ghent, Belgium (winter)	(Pashynska et al., 2002)
Glc	270	110–610	≤10	Ghent, Belgium (summer)	(Pashynska et al., 2002)
Fru	10	6–20	≤2.5	Jülich, Germany (summer)	(Kourtchev et al., 2005b)
Fru	1.4	0.3–3.9	≤10	Birkenes, Norway	(Yttri et al., 2005)
Fru	42	4.6–90	≤10	Oslo, Norway	(Yttri et al., 2005)
Fru	11	3.4–21	≤10	Elverum, Norway (winter)	(Yttri et al., 2005)
Fru	11	3.3–25	≤10	Elverum, Norway (summer)	(Yttri et al., 2005)
Fru	37	10–126	≤10	Ghent, Belgium (winter)	(Pashynska et al., 2002)
Fru	193	39–440	≤10	Ghent, Belgium (summer)	(Pashynska et al., 2002)
				Tropical (Brazil), Wet Season	
Glc & Fru	32.4	6.9–64	≤2.5	Reserva Biologica Jarú, Rondônia (1999)	(Graham et al., 2002)
Glc and Fru	48.6	17–82	≤2.5	FNS, Rondônia (1999)	(Graham et al., 2002)
Fru	4.0	2.5–5.9	≤2.5	FNS, Rondônia (2002)	(Decesari et al., 2006)
Glc	15.6	–	≤2.5	Balbina, Amazonas (day) (2001)	(Claeys et al., 2004)
Glc	0.6	–	≤2.5	Balbina, Amazonas (night) (2001)	(Claeys et al., 2004)
Glc and Fru	12.6	3.6–26	≤2.5	Balbina, Amazonas (avg) (2001)	(Graham et al., 2003b)
Glc and Fru	20	–	≤2.5	Balbina, Amazonas (day) (2001)	(Graham et al., 2003b)
Glc and Fru	5.9	–	≤2.5	Balbina, Amazonas (night) (2001)	(Graham et al., 2003b)
Glc	29	12–76	TSP	Balbina, Amazonas (1998)	(Claeys et al., 2004)
Glc	134	–	≥2.5	Balbina, Amazonas (day) (2001)	(Claeys et al., 2004)
Glc	2.7	–	≥2.5	Balbina, Amazonas (night) (2001)	(Claeys et al., 2004)
Glc and Fru	76.7	3.6–200	≥2.5	Balbina, Amazonas (avg) (2001)	(Graham et al., 2003b)
Glc and Fru	146	–	≥2.5	Balbina, Amazonas (day) (2001)	(Graham et al., 2003b)
Glc and Fru	7.2	–	≥2.5	Balbina, Amazonas (night) (2001)	(Graham et al., 2003b)

Table 5. Potassium mass concentrations in ambient air observed for different ranges of aerosol particle size (aerodynamic diameter) during the wet season in Brazil.

Average Concentration ($ng\,m^{-3}$)	Particle Diameter (μm)	Location and Time	References
24.0	0.05–1.2	FNS, Rondônia (day)	(Fuzzi et al., 2006b)
68.0	0.05–1.2	FNS, Rondônia (night)	(Fuzzi et al., 2006b)
33.5	≤2	FNS, Rondônia	(Artaxo et al., 2002)
26.2	≤2	Reserva Biologica Jarú, Rondônia	(Artaxo et al., 2002)
27.1	≤2	Reserva Biologica Jarú, Rondônia	(Guyon et al., 2003)
32.1	≤2	Ducke Forest Reserve, Amazonas (Meteorological Site)	(Artaxo et al., 1990)
26.3	≤2	Ducke Forest Reserve, Amazonas (Tower Site)	(Artaxo et al., 1990)
24.2	≤2	ZF1 site, Amazonas	(Artaxo et al., 1990)
18.0	≤2	Balbina, Amazonas	(Formenti et al., 2001)
29.2	≤2	Balbina, Amazonas	(Graham et al., 2003a)
94.0	≤2	Alta Floresta, Mato Grosso	(Echalar et al., 1998)
220.0	≤2	Alta Floresta, Mato Grosso	(Maenhaut et al., 2002)
14.0	1.2–10	FNS, Rondônia (day)	(Fuzzi et al., 2006b)
49.0	1.2–10	FNS, Rondônia (night)	(Fuzzi et al., 2006b)
76.7	2–10	FNS, Rondônia	(Artaxo et al., 2002)
73.7	2–10	Reserva Biologica Jarú, Rondônia	(Artaxo et al., 2002)
107.6	2–10	Reserva Biologica Jarú, Rondônia	(Guyon et al., 2003)
112.1	2–15	Ducke Forest Reserve, Amazonas (Meteorological Site)	(Artaxo et al., 1990)
94.6	2–15	Ducke Forest Reserve, Amazonas (Tower Site)	(Artaxo et al., 1990)
87.3	2–15	ZF1 site, Amazonas	(Artaxo et al., 1990)
69.0	2–10	Balbina, Amazonas	(Formenti et al., 2001)
52.6	2–10	Balbina, Amazonas	(Graham et al., 2003a)
270.0	2–10	Alta Floresta, Mato Grosso	(Echalar et al., 1998)
240.0	2–10	Alta Floresta, Mato Grosso	(Maenhaut et al., 2002)

Table 6. Chloride mass concentrations in ambient air observed for different ranges of aerosol particle size (aerodynamic diameter) during the wet season in Amazonia.

Average Concentration ($ng\,m^{-3}$)	Particle Diameter (μm)	Location and Time	References
5.5	≤2	FNS, Rondônia	(Artaxo et al., 2002)
5.1	≤2	Reserva Biologica Jarú, Rondônia	(Artaxo et al., 2002)
9.5	≤2	Ducke Forest Reserve, Amazonas (Meteorological Site)	(Artaxo et al., 1990)
13.0	≤2	Ducke Forest Reserve, Amazonas (Tower Site)	(Artaxo et al., 1990)
8.9	≤2	ZF1 site, Amazonas	(Artaxo et al., 1990)
65.0	≤2	Balbina, Amazonas	(Formenti et al., 2001)
4.8	≤2	Balbina, Amazonas	(Graham et al., 2003a)
2.3	≤2	Alta Floresta, Mato Grosso	(Echalar et al., 1998)
37.0	≤2	Alta Floresta, Mato Grosso	(Maenhaut et al., 2002)
14.3	2–10	FNS, Rondônia	(Artaxo et al., 2002)
9.4	2–10	Reserva Biologica Jarú, Rondônia	(Artaxo et al., 2002)
7.8	2–10	Reserva Biologica Jarú, Rondônia	(Guyon et al., 2003)
55.0	2–15	Ducke Forest Reserve, Amazonas (Meteorological Site)	(Artaxo et al., 1990)
33.2	2–15	Ducke Forest Reserve, Amazonas (Tower Site)	(Artaxo et al., 1990)
52.5	2–15	ZF1 site, Amazonas	(Artaxo et al., 1990)
155.0	2–10	Balbina, Amazonas	(Formenti et al., 2001)
59.1	2–10	Balbina, Amazonas	(Graham et al., 2003a)
41.0	2–10	Alta Floresta, Mato Grosso	(Echalar et al., 1998)
65.0	2–10	Alta Floresta, Mato Grosso	(Maenhaut et al., 2002)

Table 7. Total particulate matter mass concentrations in ambient air observed for particles with aerodynamic diameters of 1–2 μm to 10–15 μm during the wet season in Amazonia.

Mass Concentration ($\mu g\,m^{-3}$)	Particle Diameter (μm)	Location and Time	References
1.0	1.2–10	FNS, Rondônia, (DLPI, day)	(Fuzzi et al., 2006b)
4.3	1.2–10	FNS, Rondônia (DLPI, night)	(Fuzzi et al., 2006b)
1.8	1.2–10	FNS, Rondônia (MOUDI, day)	(Fuzzi et al., 2006b)
6.9	1.2–10	FNS, Rondônia (MOUDI, night)	(Fuzzi et al., 2006b)
5.7	2–10	FNS, Rondônia	(Artaxo et al., 2002)
5.1	2–10	Reserva Biologica Jarú, Rondônia	(Artaxo et al., 2002)
6.6	2–10	Reserva Biologica Jarú, Rondônia	(Guyon et al., 2003)
8.0	2–15	Ducke Forest Reserve, Amazonas (Meteorological Site)	(Artaxo et al., 1990)
7.6	2–15	Ducke Forest Reserve, Amazonas (Tower Site)	(Artaxo et al., 1990)
6.5	2–15	ZF1 site, Amazonas	(Artaxo et al., 1990)
5.8	2–10	Balbina, Amazonas	(Formenti et al., 2001)
2.8	2–10	Balbina, Amazonas (day)	(Graham et al., 2003a)
5.5	2–10	Balbina, Amazonas (night)	(Graham et al., 2003a)
16.4	2–10	Alta Floresta, Mato Grosso	(Echalar et al., 1998)
15.1	2–10	Alta Floresta, Mato Grosso	(Maenhaut et al., 2002)

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Table 8. Liquid concentrations of species ejected with AAS (Trail et al., 2005) and ABS (Webster et al., 1995) taken as representative average values for budget calculations.

Species	Buller's Drop (pg/Spore)	Ascus Sap (pg/Ascus)
Mannitol	5.3	4.7
Hexoses	3.8	nd
Potassium	nd	45.9
Chloride	nd	14.3
Solutes	9.1	64.9

nd: not determined

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Table 9. Measured and calculated concentrations of spores and related chemical components in air particulate matter from Balbina: measured number concentrations of ABS and AAS; calculated mass concentrations of solutes and spores (calculations as detailed in Sect. 4).

	ABS		AAS		AAS + ABS		
	Day	Night	Day	Night	Day	Night	Average
Spores (m^{-3})	1800	12 772	2964	7416	4764	20 188	12 476
Mannitol ($ng\,m^{-3}$)	9.5	67.7	1.7	4.3	11.2	72	41.6
Hexoses ($ng\,m^{-3}$)	6.8	48.5	nd	nd	6.8	48.5	27.7
Potassium ($ng\,m^{-3}$)	nd	nd	17.3	43.3	17.3	43.4	29.8
Chloride ($ng\,m^{-3}$)	nd	nd	5.3	13.3	5.3	13.3	9.3
Solute Mass ($ng\,m^{-3}$)	16.4	116	24.3	60.9	40.7	177	108
Spore Mass ($ng\,m^{-3}$)	118	835	592	1483	710	2318	1514

nd: not determined

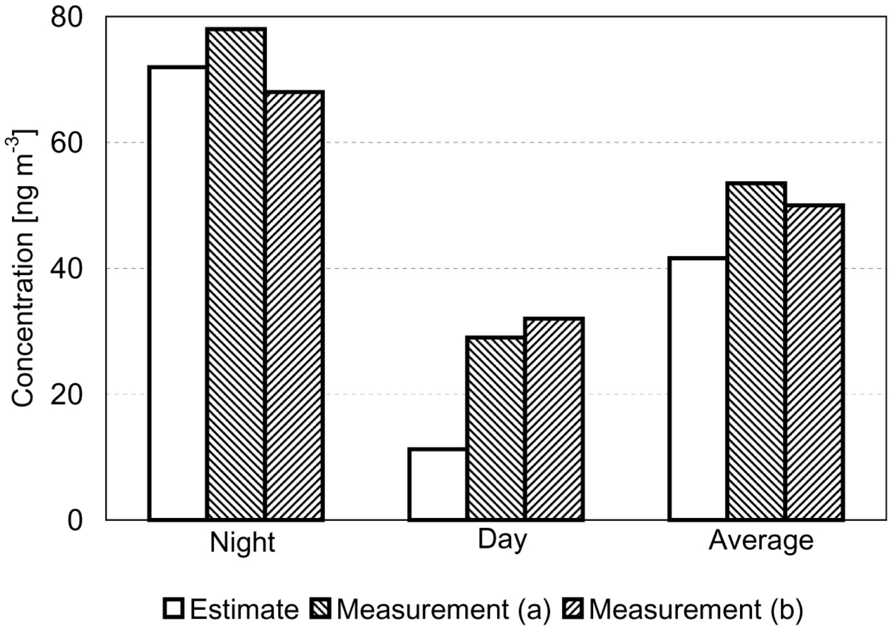

Fig. 1. Mannitol concentrations in ambient air in Amazonia (Balbina, Brazil): estimate from spore counts (this study) compared to measurements of (a) Graham et al. (2003b; plotted: mean values of 6 samples; night-time standard deviation (SD): ±15 ng m^{-3}; day-time SD: ±8 ng m^{-3}; range of diurnal average: 24–102 ng m^{-3}) and (b) Claeys et al. (2004; plotted: mean values).

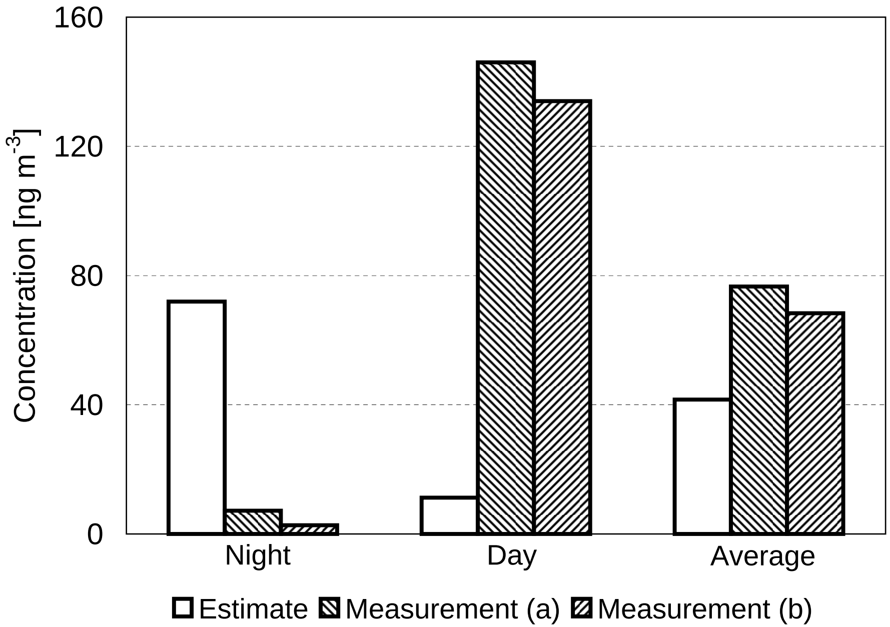

Fig. 2. Hexose (glucose and fructose) concentrations in ambient air in Amazonia (Balbina, Brazil): estimate from spore counts (this study) compared to measurements of (a) Graham et al. (2003b; plotted: mean values of 6 samples; night-time SD: ±5 ng m^{-3}; day-time SD: ±45 ng m^{-3}; range of diurnal average: 4–200 ng m^{-3}) and (b) Claeys et al. (2004; plotted: mean values).

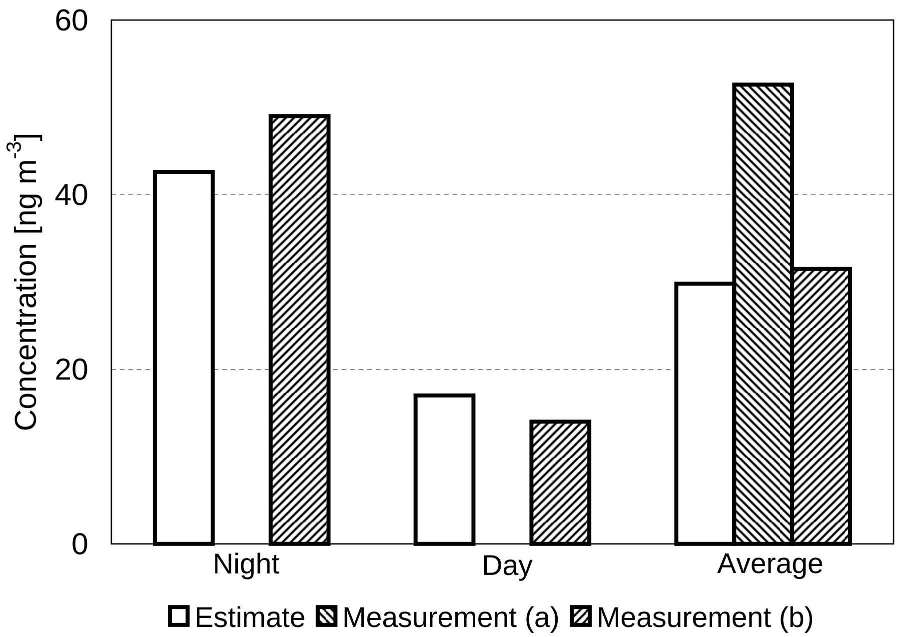

Fig. 3. Potassium concentrations in ambient air in Amazonia: estimate from spore counts at Balbina (this study) compared to measurements at (a) Balbina (Graham et al., 2003a; plotted: mean value of 8 samples; SD of diurnal average: ±29 ng m^{-3}) and (b) FNS, Rondônia (Fuzzi et al., 2006b; plotted: mean values; night-time SD: ±36 ng m^{-3}; day-time SD: ±10 ng m^{-3}).

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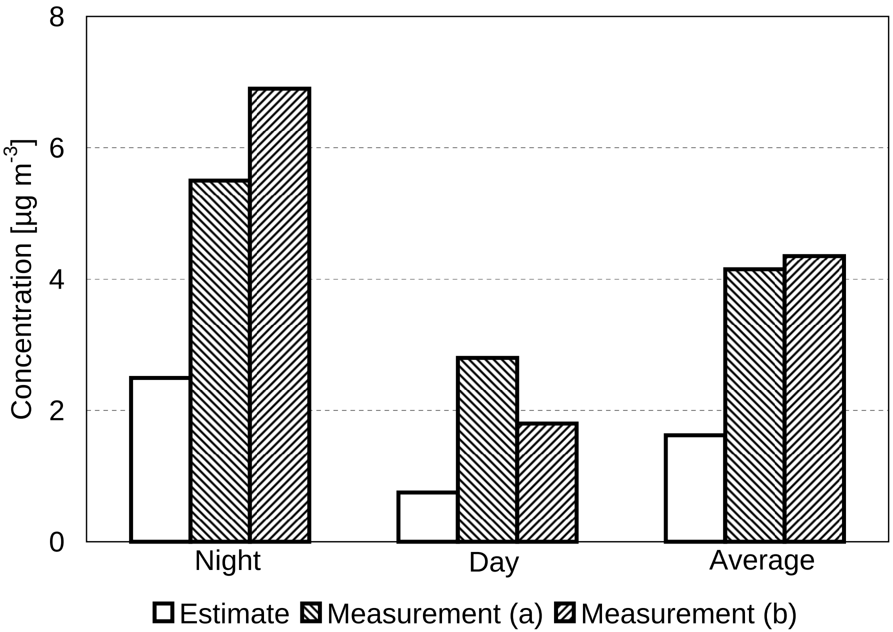

Fig. 4. Aerosol mass concentration in ambient air in Amazonia: estimate from spore counts at Balbina (this study) compared to measurements at (a) Balbina (Graham et al., 2003a; plotted: mean values) and (b) FNS, Rondônia (Fuzzi et al., 2006b; plotted: mean values; night-time SD: ±5.2 $\mu g\,m^{-3}$; day-time SD: ±1.3 $\mu g\,m^{-3}$).

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