

**High concentrations  
of biological aerosol  
particles**

J. A. Huffman et al.

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# High concentrations of biological aerosol particles and ice nuclei during and after rain

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## Abstract

Bioaerosols are relevant for public health and may play an important role in the climate system, but their atmospheric abundance, properties and sources are not well understood. Here we show that the concentration of airborne biological particles in a forest ecosystem increases dramatically during rain and that bioparticles are closely correlated with atmospheric ice nuclei (IN). The greatest increase of bioparticles and IN occurred in the size range of 2–6  $\mu\text{m}$ , which is characteristic for bacterial aggregates and fungal spores. By DNA analysis we found high diversities of airborne bacteria and fungi, including human and plant pathogens (mildew, smut and rust fungi, molds, *Enterobacteraceae*, *Pseudomonadaceae*). In addition to known bacterial and fungal IN (*Pseudomonas* sp., *Fusarium sporotrichioides*), we discovered two species of IN-active fungi that were not previously known as biological ice nucleators (*Isaria farinosa* and *Acremonium implicatum*). Our findings suggest that atmospheric bioaerosols, IN and rainfall are more tightly coupled than previously assumed.

## 1 Introduction

Micrometer-sized biological particles suspended in the atmosphere (bioaerosols) are key elements in the lifecycle of many organisms and ecosystems, and they may influence the water cycle as cloud condensation and ice nuclei (Morris et al., 2008; Després et al., 2012). Laboratory studies have shown that certain species of bacteria, fungal spores, and pollen are highly efficient IN (Maki et al., 1974; Diehl et al., 2001; Morris et al., 2012), and bioparticles have been detected in clouds, fog, rain, and snowfall (Christner et al., 2008; Pratt et al., 2009). On a global scale bioaerosols may be only a minor fraction of the total IN population (Hoose et al., 2010), but regionally bioaerosols could play an important role in the evolution of clouds and precipitation (Möhler et al., 2007), especially in pristine regions like the Amazonian rainforest (Prenni et al., 2009; Pöschl et al., 2010; Pöhlker et al., 2012b). So far, however,

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evidence linking bioaerosols with increases in IN, especially during and following precipitation, is limited (Bigg and Miles, 1964; Constantinidou et al., 1990; Allitt, 2000), and there is an apparent disconnect between concentrations of IN active biological particles commonly found on vegetation and concentrations in the air above them (Garcia et al., 2012). Airborne bioparticles are also major vectors for human, animal, and plant diseases (Pöschl, 2005; Després et al., 2012). Additionally, pollen and spores have been suggested to enhance asthma, allergies and other respiratory conditions during thundershowers (Taylor and Jonsson, 2004), but little evidence for a related increase of bioaerosol concentrations has been reported (Dales et al., 2012).

During the BEACHON-RoMBAS intensive field campaign (<http://cires.colorado.edu/jimenez-group/wiki/index.php/BEACHON-RoMBAS>) we performed comprehensive bioaerosol measurements during summertime in a semi-arid North American pine forest (20 July to 23 August 2011, Manitou Experimental Forest 35 km northwest of Colorado Springs, CO, USA, 2370 m a.s.l.). The biological, chemical and physical measurement techniques applied include: online fluorescence detection (ultraviolet aerodynamic particle sizer, UV-APS; waveband integrated bioaerosol sensor, WIBS); scanning electron microscopy (SEM) and epifluorescence microscopy (FM); real-time IN counting in a continuous flow diffusion chamber (CFDC) and microscopic IN activation experiments; aerosol filter and impactor sampling; and DNA analysis for biological speciation. To our knowledge, this study provides the most comprehensive and detailed data set of time- and size-resolved atmospheric bioaerosol properties available to date, and is unique in the availability of comprehensive real-time and off-line IN measurement data for comparison.

## 2 Materials and methods

Aerosol measurements were performed using inlets mounted 1–4 m a.g.l. During rain periods, all measurements discussed refer to particles not embedded in rain droplets.

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Below is a brief discussion of materials and methods of sampling and analysis utilized. Additional details are presented in the Supplement.

## 2.1 Meteorological and leaf moisture measurements

Precipitation occurrence, rate and microphysical state (i.e. rain versus hail) was measured using a laser-optical disdrometer (PARTicle Size and VELOCITY "PARSIVEL" sensor; OTT Hydromet GmbH, Kempton, Germany). Leaf wetness state was characterized using a dielectric Leaf Wetness Sensor (LWS; Decagon Devices, Inc.). The LWS detects and provides a relative measure of the water or ice content on or near the sensor surface (within  $\sim 1$  cm) by measuring the dielectric constant of the surface. The sensor outputs a voltage (measured in millivolts, mV) which is directly proportional to the amount of water or ice in or near the sensor upper surface.

## 2.2 Online fluorescence measurements

An ultraviolet aerodynamic particle sizer (UV-APS; TSI Inc. Model 3314, St. Paul, MN) was utilized for this study following previously described procedures (Huffman et al., 2012). The instrument provides aerodynamic diameter ( $D_a$ ) of aerosol particles in the range of 0.54–19.81  $\mu\text{m}$  and total fluorescence (420–575 nm; non-wavelength-dispersed) of particles after pulsed excitation ( $\lambda_{\text{ex}} = 355$  nm). Also utilized was the waveband integrated bioaerosol sensor – model 4 (WIBS4; University of Hertfordshire), a dual-channel fluorescence spectrometer (Kaye et al., 2005) providing size, asymmetry, and fluorescence of individual particles. Fluorescence is measured in three emission channels after Xe lamp pulses at 280 nm and 370 nm.

A subset of the WIBS4 single particle data (8000 particles) was analyzed using hierarchical agglomerative cluster analysis using a group average distance metric (Robinson et al., 2012). Bioaerosol fluxes were then estimated for each cluster by combining the concentration gradient with vertical wind speed data (see Supplement for more details). Fluorescent particles ( $N_f$ ) detected by the UV-APS and WIBS can be regarded as

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a lower limit for the abundance of primary biological aerosol particles (Huffman et al., 2010; Pöhlker et al., 2012a), probing fluorophores such as NAD(P)H, riboflavin, and tryptophan.

### 2.3 Filter and impactor aerosol samples

Coarse-mode particles were collected using a variety of filter and impactor sampling techniques from two adjacent inlets (4 m above ground), unless otherwise noted. Size-resolved particle samples were collected using a micro-orifice uniform deposition impactor (MOUDI; MSP model 110-R) at a flow-rate of 30 LPM via a dedicated inlet. Samples used for offline ice nucleation analysis were collected onto siliconized, hydrophobic glass slides (Hampton Research, HR3-2125). Size cuts at each plate are listed in the SOM. Total aerosol samples were collected onto glass cover slides (13 × 13 mm) coated with a thin layer of high viscosity grease installed in a home-built, single-stage impactor (Flow-rate 1.2 LPM,  $D_{50}$  cut 0.5  $\mu\text{m}$ ). Aerosol samples for electron microscopy analysis were collected with a stacked filter housing using 12 mm diameter gold-coated Nuclepore<sup>®</sup> polycarbonate filters with pore sizes of 2  $\mu\text{m}$  for coarse particles and 0.2  $\mu\text{m}$  for fine particles, respectively. Total aerosol samples for DNA analysis were collected onto 150 mm glass fiber filters (Machery-Nagel, Type MN 85/90, 406015) using a self-standing high-volume sampler (Digitel DHA-80) operated at 1000 LPM and located approximately 50 m from the sampling trailer. Size-resolved viable bioparticles were collected directly into growth media using an Andersen six-stage cascade impactor for subsequent DNA analysis of viable organisms.

### 2.4 Off-line sample analysis

Fluorescence microscopy images were taken on a BZ-9000 Fluorescence Microscope (Keyence, Inc., Osaka, Japan). The instrument was equipped with a super high-compression mercury lamp (120 W) and a 2/3-inch, 1.5 mega pixel monochrome CCD. DAPI-BP (blue), FBP-BP (green), and TexasRed (red) filters were used. Filter details,

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including wavelength ranges, are detailed in the SOM. Scanning electron microscopy (SEM) images were acquired using the secondary electron in-lens detector of a high-performance field emission instrument (LEO 1530 FESEM, EHT 10 keV, WD 9 mm). The elemental composition of inorganic components was characterized using the Oxford Instruments ultra-thin-window energy-dispersive X-ray (EDX) detector.

Optimized methods of DNA extraction, amplification, and sequence analysis of the internal transcribed spacer (ITS) regions were used to determine bacterial and fungal diversity from the high-volume air filter samples (Fröhlich-Nowoisky et al., 2009, 2012). For bacteria, the 16S ribosomal gene was first amplified for taxonomic identification with primer pairs 9/27f and 1492r under PCR conditions and then cloned and sequenced (Weisburg et al., 1991, 2007). The same primer pair was used for the bacterial lysates obtained from Andersen sampler culture plates. The primer pair ITS4Oo and ITS5 (Nikolcheva and Bärlocher, 2004) was used for amplification of *Peronosporomycetes* (formerly *Oomycota*). Also specific for this study, the ITS regions from fungal lysates, obtained from the cultivation experiments of Andersen impactor samples, were amplified with the primer pair ITS4 and ITS5 (White et al., 1990; Fröhlich-Nowoisky et al., 2009, 2012). The obtained PCR products were sequenced using the primer ITS5 and sequence analysis was performed as described previously (Fröhlich-Nowoisky et al., 2009, 2012). The sequences from the obtained operational taxonomic units have been deposited in the GenBank database under following accession numbers: JX135610–JX136661 (fungi), JX228219–JX228862 (bacteria), and JQ976038–JQ976273 (*Peronosporomycetes*).

Fungal and bacterial colonies were picked and cultured in DPY medium (dextrose  $10\text{ g L}^{-1}$ , peptone  $3\text{ g L}^{-1}$ , yeast extract  $0.3\text{ g L}^{-1}$ ) in 96-well polypropylene plates and incubated at  $16^\circ\text{C}$ . A  $50\ \mu\text{L}$  aliquot of DPY media containing hyphal fragments and fungal spores was tested from each well for ice nucleation activity in a temperature range  $-12^\circ\text{C}$  to  $-2^\circ\text{C}$  (Garcia et al., 2012).

Freezing properties of particles collected on hydrophobic MOUDI slides were determined with an optical microscope and a flow cell with temperature and relative humidity

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control (Dymarska et al., 2006; Iannone et al., 2011). The RH was first set to  $> 100\%$  to condense water droplets on the particles. The droplets were grown to approximately  $100\ \mu\text{m}$  in diameter, and after droplet growth was completed each droplet contained between 30 and 100 particles. Then the temperature was decreased at a rate of  $10\ \text{K min}^{-1}$  until a temperature of  $-40\ ^\circ\text{C}$  was reached. Progression of ice formation was monitored continuously using a camera system.

## 2.5 Real-time IN detection

A ground-based version of the Colorado State University continuous flow diffusion chamber (CFDC) (Rogers et al., 2001) was employed for real-time measurements of IN concentrations. The CFDC permits observation of ice formation on a continuous stream of particles at controlled temperatures and humidities. Physical impaction of larger particles ( $> 2.4\ \mu\text{m}$ ) in advance of the CFDC prevents false detection of large particles as IN. We note that removing these larger particles upstream of the CFDC likely removes some particles that can potentially serve as IN, however, field data suggests that this underestimation is normally less than a factor of two under most sampling situations (Garcia et al., 2012). Water supersaturated conditions (relative humidity  $\sim 105\%$  with respect to water) were typically used for CFDC processing to emphasize ice nucleation predominantly by a condensation/immersion freezing process (Sullivan et al., 2010). Ice crystals activated as IN in the CFDC were collected via impaction at the CFDC outlet (Prenni et al., 2009, 2013; Garcia et al., 2012).

## 3 Results and discussion

During the field campaign, we observed frequent transitions between dry background conditions and rain events. Figure 1 shows characteristic meteorological parameters and aerosol particle concentrations for seven consecutive days during the campaign (31 July to 6 August 2011). During dry periods we observed low concentrations of both

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fluorescent bioparticles ( $N_{F,c} \approx 30 \text{ L}^{-1}$ ) and total aerosol particles ( $N_{T,c} \approx 300 \text{ L}^{-1}$ ) in the supermicrometer size range, as detected by the UV-APS. At the onset of every rain event, the fluorescent bioparticles exhibited an immediate steep increase by as much as 60–160 % per minute during the first ten minutes of precipitation (Fig. 1b). The total concentration of coarse particles ( $> 1 \mu\text{m}$ ), including non-fluorescent material, increased less dramatically but also substantially (by 10–65 % per minute, Fig. 1c), which is in contrast to the traditional view of atmospheric aerosol processing that assumes efficient removal of large aerosol particles by precipitation. Our online measurements, however, show that the concentration of coarse aerosol particles not embedded in rain droplets can rapidly rise by factors as high as  $\sim 4$  to  $\sim 12$  and remain elevated over multiple hours, depending on the intensity and duration of the rain event. Heavy downpours produced a large and extended increase in particle concentration, but even light drizzle led to substantial enhancements (up to factor  $\sim 4$ ). The strong increase of total and biological particle concentrations implies that the precipitation-related enhancements of particle sources as specified and discussed below were substantially stronger than the precipitation-related particle sinks (i.e. precipitation scavenging).

The number fraction of fluorescent bioparticles in total supermicron particles detected by the UV-APS was  $\sim 2$ –6 % under dry conditions (Fig. 1d). It jumped to  $\sim 20$  % at the onset of rainfall, and it increased further to  $\sim 40$  % when humid conditions with elevated leaf wetness persisted beyond the actual rainfall, which was mostly the case during nighttime after strong daytime precipitation (Fig. 1a). The UV-APS, however, provides only a lower limit proxy for the overall abundance of bioparticles, because it is designed for online detection of viable bacteria with strong autofluorescence at specific wavelengths (Huffman et al., 2012; Pöhlker et al., 2012a). Microscopic investigations, making use of a wider range of wavelengths as well as morphological characteristics and elemental composition data (FM, SEM), indicate that the relative abundance of bioparticles in the supermicron size range during rain events (i.e. during or after rainfall) was as high as 55–80 %. In contrast, mineral dust particles prevailed during dry periods (70–80 %, Tables 1–2). Figure 2a, b show microscopic images of aerosol

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impactor samples clearly highlighting the contrast between the relatively weak red fluorescence from irregularly shaped dust in a sample collected during dry weather and the intense green and blue fluorescence from cellular structures in a sample collected during a rain event.

5 During rainfall the median diameter of fluorescent bioparticles was usually 2–3  $\mu\text{m}$ , and the concentration of these particles decayed swiftly after the precipitation had stopped (Fig. 1e). When humid conditions with elevated leaf wetness persisted beyond the actual precipitation, larger fluorescent bioparticles with a median diameter around 4–6  $\mu\text{m}$  appeared ca. 8 h after the beginning of rainfall and persisted for up to 12 more hours (Fig. 1e). Statistical cluster analysis of the size, asymmetry, and multi-channel fluorescence data recorded with the WIBS instrument confirmed that the smaller bioparticles enhanced during rainfall were qualitatively different from the larger ones enhanced after rainfall, implying different sources or physiological states (Pöhlker et al., 2012a; Robinson et al., 2012).

15 The 2–3  $\mu\text{m}$  bioparticles present through-out the rainfall are likely bacteria or fungal spores released from surrounding vegetation surfaces through mechanical agitation by raindrops (Faulwetter, 1917; Hirst and Stedman, 1963), which is consistent with the observed strong initial enhancement at the onset of rain and a less pronounced enhancement during continued rainfall and immediately following events (e.g.: 2 August, Fig. 1a–c). The increase of relative humidity and leaf wetness can also trigger other bioparticle emission mechanisms like the active wet ejection of fungal spores (Hirst and Stedman, 1963; Elbert et al., 2007; Després et al., 2012) or hygroscopic swelling-induced pollen fragmentation (Taylor et al., 2004; Miguel et al., 2006; Pöhlker et al., 2013; Pummer et al., 2012). Moreover, bioparticles observed during rainfall may also have precipitated from clouds in which some of them served either as giant cloud condensation nuclei (GCCN) or ice nuclei contributing to rain formation (Sands et al., 1982; Morris et al., 2004; Christner et al., 2008; Garcia et al., 2012).

25 The 4–6  $\mu\text{m}$  bioparticles observed during the humid post-rain periods appear to have been freshly emitted from active biota growing on wetted terrestrial surfaces near the

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measurement location, e.g. spores ejected by fungi, lichens and other cryptogamic covers growing on soil, rock and vegetation (Elbert et al., 2007; Elbert et al., 2012). The attribution of the larger post-rain bioparticles to local sources is consistent with co-located concentration gradient measurements suggesting a net upward flux of fluorescent bioparticle emission after rainfall ( $\sim 50\text{--}500\text{ m}^{-2}\text{s}^{-1}$ ), in range with earlier estimates of bioparticle emission fluxes (also Lindemann et al., 1982; Elbert et al., 2007; Burrows et al., 2009; Després et al., 2012).

DNA analyses of aerosol samples collected during the campaign yielded over 5000 sequences that could be attributed to  $\sim 1000$  different operational taxonomic units, or species of bacteria, fungi, and other organisms. The species richness and the frequency of occurrence of both bacteria and fungi were higher by factors of 2–10 in aerosol samples collected under wet conditions (periods including rainfall or humid post-rain periods) than under dry conditions. Similar to other rural continental regions, most bacterial species were from *Proteobacteria*, *Actinobacteria*, *Firmicutes* and *Bacteroidetes* (Després et al., 2012). Most fungal species were from *Basidiomycota* (club fungi) and *Ascomycota* (sac fungi; Fröhlich-Nowoisky et al., 2009, 2012). The identified groups of microorganisms comprise a number of plant pathogens and human allergens (mildew, smut and rust fungi, molds, *Enterobacteraceae*, *Pseudomonadaceae*). These findings provide a rationale for reported enhancements of asthma and other respiratory diseases during rain showers (Taylor and Jonsson, 2004; Dales et al., 2012).

To characterize the ice nucleating ability of aerosol particles during rain events and dry periods, we present CFDC real-time measurements of IN activity at  $-25^\circ\text{C}$  for particles  $< 2.4\ \mu\text{m}$ , as well as microscopic IN activation experiments of samples collected with a cascade impactor resolving a size range of  $0.3\text{--}18\ \mu\text{m}$  and a temperature range of  $-10^\circ\text{C}$  to  $-40^\circ\text{C}$ . During rain events, the IN concentrations measured in the CFDC were an order of magnitude higher than during dry periods and followed a close linear correlation with fluorescent bioparticle concentration that was not observed under dry conditions (Fig. 2e vs. 2f) (Prenni et al., 2013). The microscopic experiments showed that aerosol samples collected during rain events exhibited the strongest IN activation

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at temperatures above  $-20^{\circ}\text{C}$  and sizes around  $1.8\text{--}5.6\ \mu\text{m}$  (Figs. 3 and S1), which are common for biological ice nucleators such as bacteria and fungal spores. During these periods as much as  $\sim 1\%$  ( $\sim 0.5\ \text{L}^{-1}$ ) of supermicron particles were IN-active at  $-15^{\circ}\text{C}$  (Fig. S2). In contrast, the aerosol samples collected during dry weather and dominated by dust exhibited the strongest IN activation only below  $-20^{\circ}\text{C}$  for all size classes (Figs. 3 and S1), and the fraction of supermicron particles IN-active at  $-15^{\circ}\text{C}$  was much lower ( $< 10^{-4}$ ), as expected for mineral dust (Möhler et al., 2006; Connolly et al., 2009; DeMott et al., 2010a; Hoose and Mohler, 2012).

The size distribution of IN that activated at  $-15^{\circ}\text{C}$  exhibits a distinct peak in the range  $2\text{--}6\ \mu\text{m}$  that coincides with the peak of the size distribution of fluorescent bioparticles observed during rain events (Fig. 2d). The correlations between IN and FBAP number concentrations and size distributions (Fig. 2d, f), as well as the temperature dependence of IN activation (Figs. 3 and S1), suggest that bioparticles account for the observed increase of IN during rain and that both the  $2\text{--}3\ \mu\text{m}$  particle mode directly associated with rainfall and the  $4\text{--}6\ \mu\text{m}$  particle mode associated with humid post-rain periods comprise highly efficient IN. Indeed, IN-active bacteria of the genus *Pseudomonas* sp., known to have activation temperatures up to  $-4^{\circ}\text{C}$  (Morris et al., 2004), were found by the combination of cultivation experiments, freezing tests, and DNA analyses of aerosol samples in the size range of  $\sim 1\text{--}4\ \mu\text{m}$ . Using the same combination of tests we also found the fungal species *Fusarium sporotrichioides*, which is known to be IN active at  $-10^{\circ}\text{C}$  to  $-8^{\circ}\text{C}$  (Richard et al., 1996), and two previously unknown IN-active fungi from the phylum of *Ascomycota*: *Isaria farinosa* and *Acremonium implicatum* (Fig. 4). The IN-active fungi were cultivated and produced spores that are fluorescent, exhibit diameters in the range of  $1\text{--}4\ \mu\text{m}$ , and induce freezing at  $-12^{\circ}\text{C}$  to  $-5^{\circ}\text{C}$ . Overall, the DNA analyses of aerosol samples collected during rain events showed higher diversity and frequency of occurrence for bacteria and fungi from groups that comprise IN active species (*Pseudomondaaceae*; *Sordariomycetes*). Identification of both *Pseudomonas* sp. and *Sordariomycetes* directly from IN samples collected using the CFDC during rain shows conclusively that the biological particles were indeed

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active as ice nuclei. Convective lofting of biological IN active at temperatures of  $-15^{\circ}\text{C}$  and warmer, where ice mass growth rates maximize (Korolev, 2007) and freezing of larger drops can initiate secondary ice generation (Hallett and Mossop, 1974), may invigorate the glaciation of mixed-phase clouds and thus may strongly contribute to the formation of precipitation.

## 4 Conclusions

Our observations indicate that rainfall can trigger intense bursts of bioparticle emission and massive enhancements of atmospheric bioaerosol concentrations by an order of magnitude or more, from the onset of precipitation through extended periods of high surface wetness after the rainfall (up to one day). The strong contrast against low background concentrations under dry conditions suggests that the repeated bursts of bioparticle release during and after rain may play an important role in the spread and reproduction of microorganisms in certain environments, and may also contribute to the atmospheric transmission of pathogenic and allergenic agents (Fig. 5). To quantify these effects, we suggest comprehensive metagenomic analyses and dispersion studies of atmospheric bioaerosols contrasting different meteorological conditions. Follow-up studies in other environments shall elucidate whether the observed rain-related bioaerosol increase is a common feature of terrestrial ecosystems or specific for the investigated semi-arid environment.

Three key results of our measurements during rain and dry periods indicate the critical and dynamic role of bioaerosols as IN sources that may strongly influence the evolution of cloud microphysics and precipitation processes: (1) large and closely correlated increases of bioparticles and IN during rain events; (2) similar size distribution patterns of rain-enhanced bioparticles and IN active in the warmest regime of mixed-phase clouds ( $\geq -15^{\circ}\text{C}$ ); and (3) identification of IN-active bioparticles in aerosol and IN samples collected during rain events. Rainfall that triggers bioparticle emission may seed further precipitation (Bigg and Miles, 1964) by convective lifting of bioparticles into

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clouds where they can serve as IN, inducing cold rain formation (Hallett and Mossop, 1974; Korolev, 2007), or as GCCN, inducing warm rain formation (Möhler et al., 2007; Pöschl et al., 2010; Després et al., 2012). However, more detailed vertical transport and vertical profile information about rain-related effects will be critical to understanding what the impact of rain-initiated bioaerosol production could mean at the cloud level and for cloud formation. Recent studies suggested that bioaerosols play crucial roles in the hydrological cycle and evolution of pristine tropical rainforest ecosystems (Prenni et al., 2009; Pöschl et al., 2010; Pöhlker et al., 2012b). The measurement results of this study suggest that bioaerosols may also play an important role in mid-latitude semi-arid forest ecosystems, consistent with the recent observation that biogenic emissions significantly impact CCN in the region (Levin et al., 2012). Accordingly, deforestation and changes in land-use and biodiversity might have a significant influence on the abundance of IN, the microphysics and dynamics of clouds and precipitation in these regions, and thus on regional and global climate (DeMott et al., 2010b). In-cloud measurements of aerosol and hydrometeor composition, aerosol- and cloud-resolving process model studies, and earth system model studies capturing potential feedbacks between the atmosphere and biosphere will be required to further quantify the relevance of these effects for climate prediction.

**Supplementary material related to this article is available online at:**

**<http://www.atmos-chem-phys-discuss.net/13/1767/2013/acpd-13-1767-2013-supplement.pdf>.**

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**Table 1.** Number fraction of biological particles and mineral dust particles in aerosol samples collected during dry periods and rain events. The sample numbers S10, S12, S20, S23 refer to Nuclepore<sup>®</sup> filters analyzed by SEM (details specified in Sects. S1.5.1.4 and S1.5.3). The UV-APS data were averaged over periods matching the filter sample collection times. Fluorescent biological aerosol particles (FBAP), primary biological aerosol particles (PBAP).

Method (Particles)	Dry		Rain	
	S10	S12	S20	S23
UV-APS (FBAP/Total)	0.04	0.06	0.28	0.20
SEM (PBAP/Total)	0.03	0.07	0.78	0.56
SEM (Dust/Total)	0.80	0.76	0.08	0.38

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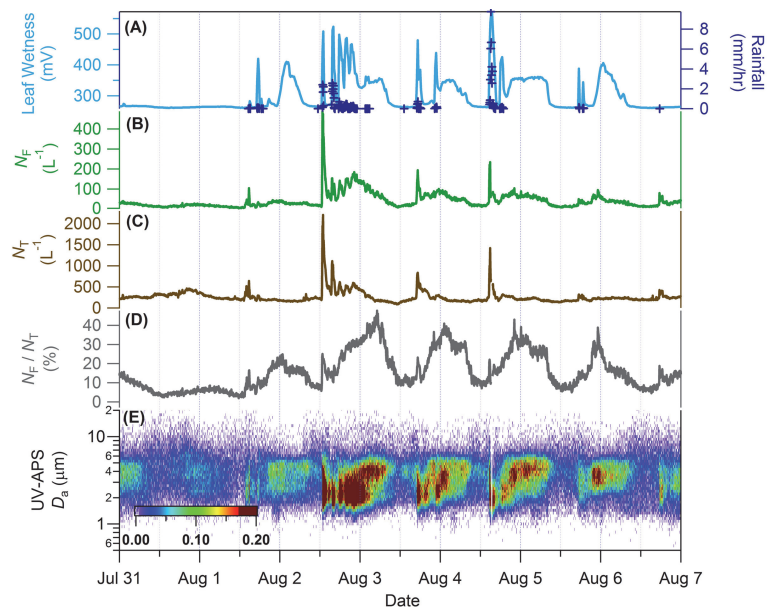


**Table 2.** Number fraction of bioparticles on MOUDI stages 4 (3.2–5.6  $\mu\text{m}$ ) and 5 (1.8–3.2  $\mu\text{m}$ ) of aerosol samples collected during a dry period (M28) and a rain event (M10). See Supplement Sect. S1.5.1.1 for sampling dates. Estimates based on fluorescence microscopy.

	Dry (M28)		Rain (M10)	
	Stage 4	Stage 5	Stage 4	Stage 5
Number fraction	0.25	0.22	0.79	0.67

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**Fig. 1.** Time series of measurement data showing repeated bursts of airborne biological particles with rain events. **(A)** Measured rainfall (dark blue crosses) and corresponding leaf wetness (light blue trace). **(B)** Concentrations ( $L^{-1}$ ) of supermicron fluorescent bioparticles ( $N_F$ ) and **(C)** total ( $N_T$ ) supermicron particles. **(D)** Fraction of fluorescent biological to total ( $N_F/N_T$ ). **(E)** Size-resolved fluorescent bioparticle concentrations measured with the UV-APS instrument (color bar:  $dN_i/d\log D_a$ ,  $L^{-1}$ ). Data are plotted against local time (mountain daylight time, MDT).

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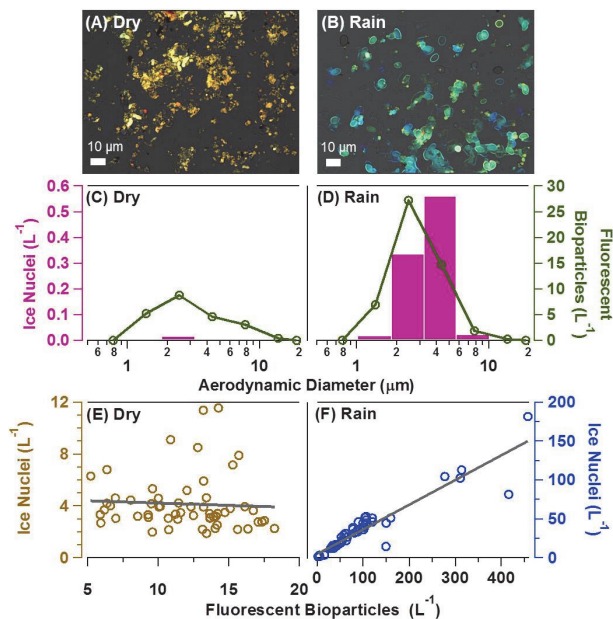
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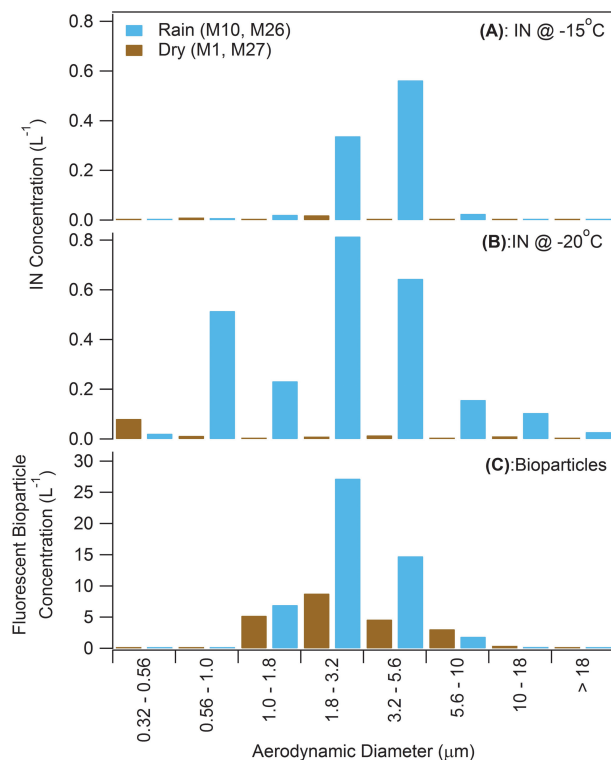
**Fig. 2.** Contrasting aerosol properties during dry periods and rain events. **(A, B)** Fluorescence microscope images of aerosol impactor samples. **(C, D)** Size distributions of ice nuclei observed at  $-15^{\circ}\text{C}$  in microscopic IN activation experiments (bars, left axis) and of fluorescent bioparticles detected by UV-APS (traces, right axis). **(E, F)** Number concentrations of ice nuclei observed at  $-25^{\circ}\text{C}$  in CFDC measurements plotted against fluorescent bioparticles detected by UV-APS (particle diameter  $< 2.4\ \mu\text{m}$ ). The displayed linear fits yield  $R^2$  correlation coefficients of **(E)** 0.003 and **(F)** 0.88.

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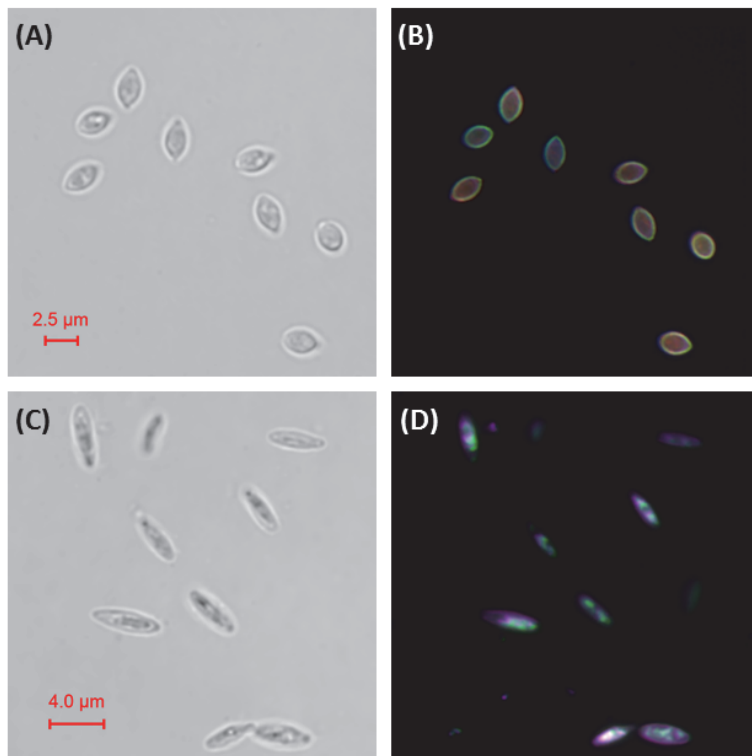

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**Fig. 3.** Size distributions of ice nuclei observed in microscopic IN activation experiments **(A)** at  $-15^{\circ}\text{C}$  and **(B)** at  $-20^{\circ}\text{C}$  for aerosol impactor samples collected during dry periods and rain events. **(C)** Size distribution of bioparticles measured by UV-APS during the same periods. See Supplement Sect. S1.5.1.1 for sampling dates.

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**Fig. 4.** Fluorescence microscopy images of fungal spores from lab cultivation of the two fungi (*Ascomycota*) with previously unknown IN activity: **(A–B)** *Isaria farinosa*, **(C–D)** *Acremonium implicatum*. Left panels show bright-field image and right panels show overlay of red, green, and blue fluorescence.

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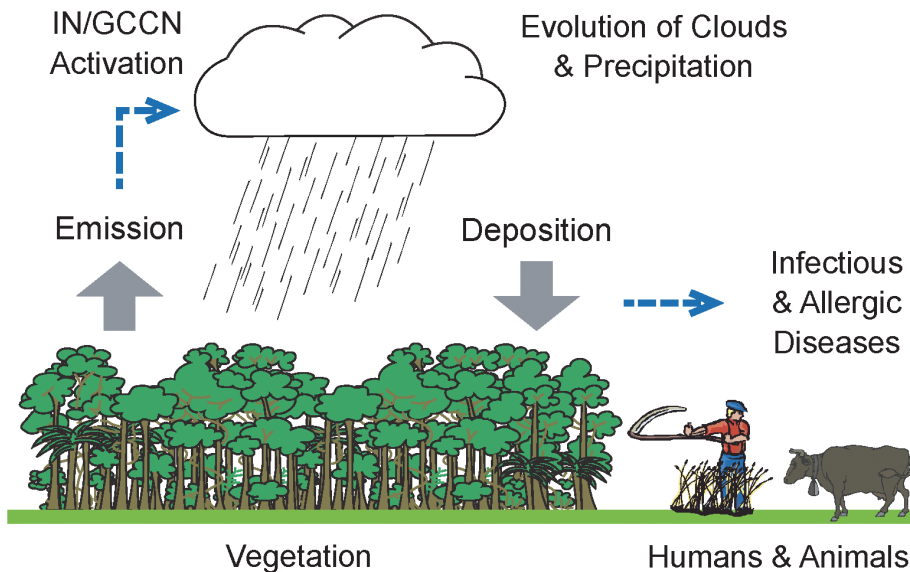
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**Fig. 5.** Coupling and effects of biological aerosol particles and precipitation: rain can enhance bioparticle emissions (rain splash, active wet discharge, etc.); bioparticles serving as ice nuclei or giant cloud condensation nuclei (IN/GCCN) can influence the evolution of clouds and precipitation; deposition of pathogenic and allergenic species can trigger human, animal and plant diseases.

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