

Emission rate of charged spores in basidiomycetous fungi and the relaxation time of their electric charges

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Abstract Basidiospores are one of the main components of coarse fraction of atmospheric aerosol. Majority of them, the ballistospores of 20,000 species of Basidiomycotina, carry electrostatic charges when getting airborne. To study the polarity and magnitude of primary charges and the hymenial emission rate of charged spores, 128 spore samples of 31 species of Agaricomycetes were collected in natural conditions. A portable device was placed under the fruiting body and the freely falling charged spores were extracted from the air by a horizontal homogeneous electrostatic field. The charge polarity distribution was the same in all intraspecies spore samples; it was unipolar-positive, unipolar-negative, or bipolar, depending on the species. The mean spore charge magnitude was 21–981 e, and it was not related to the emission rate of charged spores. The hymenial emission rate was fluctuating, and the maximum value was 715 charged spores $\text{cm}^{-2} \text{s}^{-1}$. To estimate the territorial emission rate of charged spores, area of the hymenial surface per hectare of forest was calculated for three species and the maximum values were 11 $\text{m}^2 \text{ha}^{-1}$ and

8.6×10^7 charged spores $\text{ha}^{-1} \text{s}^{-1}$. Calculations showed that a spore charge diminished sevenfold within 47 min. Ecologists, health and agricultural scientists could be interested in this information. It could be useful by investigating the role of microorganisms in meteorological phenomena and in atmospheric processes in general.

Keywords Agaricomycetes · Ballistospore · Charge-to-mass quotient · Electric charge · Emission rate · Charge relaxation time

1 Introduction

Contribution of fungal spores to the biogenic aerosol particles in the atmosphere has been studied for a long time (Gregory 1973); at present, it is carried out at the level of continent, forest, and fruitbody (Galante et al. 2011; Winiwarter et al. 2009; Zhang et al. 2010). There is a swath of research on spore concentrations in the ambient air often put in the context of human health and indoor air quality (Delfino et al. 1997; Fairs et al. 2010; Neas et al. 1996). This shows, for example, that fungal spores, especially basidiospores, are among the important triggers of asthma exacerbations needing emergency visits (Dales et al. 2000). But the role of fungal spores and other microorganisms in the meteorological phenomena and atmospheric processes

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in general is an underexplored component in researches in atmospheric and climate sciences (Morris et al. 2011). It is important to go beyond the description of abundance of microorganisms in the atmosphere toward an understanding of their dynamics in terms of both biological and physicochemical properties and of their relevant transport processes at different scales (Morris et al. 2011).

Atmospheric aerosol particles modify the chemical composition of atmospheric gas-phase and particulate matter due to the collision–coalescence processes and the absorption of molecules from surfaces. These effects of atmospheric aerosol particles are dependent on their concentration, size, chemical composition, and electric charge (Seinfeld and Pandis 2006; Hirsikko et al. 2010). Charged airborne molecules, molecule clusters, and the finest aerosol particles (<7 nm in diameter) are typically singly charged (Hirsikko et al. 2010). The largest particles, being in the steady state of bipolar charging with atmospheric ions in the atmosphere where the equal concentrations of positive and negative ions occur, carry several elementary charges on average. Particles with the diameter of 2 µm carry ~3 e, particles with 5 µm carry ~5 e, and particles with 10 µm carry ~7 e [according to the Boltzmann equilibrium equation (Roos 1996)]. These charges are distributed symmetrically in sign. Ballistic basidiospores [2–16 µm in diameter (Ingold 2001)] (further in the text as “spores”), at the moment of release from a fungal fruitbody into the atmosphere, carry on average tens to thousand elementary charges; in a spore sample, the polarity distribution of charges is unipolar-positive or unipolar-negative, or bipolar (Saar 2013). Anemophilous pollen grains (10–100 µm in diameter) carry thousands elementary charges on average at a moment of release from an inflorescence; in a grain sample, the polarity distribution of charges is bipolar (Bowker and Crenshaw 2007).

Essential differences between old atmospheric aerosol particles and freshly emitted basidiospores and pollen grains occur in the polarity distribution of charges and the magnitude of charges. Whether these biological particles could be capable of modifying the electrical characteristics of the lowest layer of the atmosphere is potentially interesting topic of study. To investigate the contribution of spores, we have to know the emission rate of charged spores in space unit, charges on spores, the time during which the spores

retain a substantial portion of this primary charge during spore transport by air flows, and the height of the atmospheric layer in which these spores could be present. Information about these factors is absent or scanty in the literature. The emission rate of charged spores and the height of atmospheric layer have received no attention until now. The retaining or relaxation time is assessed for pollen grains (Bowker and Crenshaw 2003) but not for spores. The spore charges measured in the whole and healthy fruitbodies growing in their natural habitats are shown for only five species (Swinbank et al. 1964; Saar 2013). In the present article, we explored all these factors, except the height of atmospheric layer.

To study the relaxation time, we developed a theoretical model and made an estimation using data on air ions in Estonia. To explore the charges and the emission rate of charged spores, we integrated available information from several investigations carried out earlier in natural forest conditions in Estonia on the following subjects: the magnitude and polarity of spore charges in hymenomycetous Agaricomycetes, relative amount of trees affected by a polypore and fruitbody number per tree, seasonal dynamics of fruitbody production in mushrooms and spore production in polypores. Based on these data, we tested the following hypotheses: (1) all ballistosporic fungi of Agaricomycetes exhibit primary electric charges on basidiospores; (2) these charges depend on the fungal species; (3) fruitbodies emit charged spores (and charges) at variable rates; (4) emission rate of charged spores from a unit area of forest depends on the type of forest.

2 Materials and methods

2.1 Collection of spores

Spores were collected in chambers that were placed adjacent to the hymenial surface of fruitbodies growing in natural forest conditions of Järvselja (58°16'N, 27°18'E) in 1973, in Tammistu (58°27'N, 26°55'E) in 1974, and in Koke (58°18'N, 26°55'E) in 1978 as described in Saar (2013). Spore collecting lasted from 15 to 1,500 min and was performed during different annual (vernal, estival, autumnal) and circadian (nocturnal, morning, diurnal, evening) periods. Altogether 31 macrofungi species inhabiting standing and

downed wood, litter, woody debris, decomposed organic matter, and soil were included in the present study. These species represented the Agaricales, Boletales, Cantharellales, Corticiales, Hymenochaetales, Polyporales, Russulales, and Thelephorales orders (Agaricomycetes, Basidiomycota), covering 19 families and 26 genera. Three types of hymenophore (configuration of the spore-producing surface) were represented: the poroid hymenophore by *Fomes fomentarius* (L.) J. Kickx f., *Fomitopsis pinicola* (Sw.) P. Karst., *F. rosea* (Alb. & Schwein.) P. Karst., *Ganoderma applanatum* (Pers.) Pat., *Junghuhnia nitida* (Pers.) Ryvarden, *Phellinus alni* (Bondartsev) Parmasto, *P. nigricans* (Fr.) P. Karst., *P. populicola* Niemelä, *P. tremulae* (Bondartsev) Bondartsev & P.N. Borisov, *Piptoporus betulinus* (Bull.) P. Karst., *Polyporus badius* (Pers.) Schwein., and *Suillus luteus* (L.) Roussel, the lamellate hymenophore by *Amanita muscaria* (L.) Lam., *Cantharellus cibarius* Fr., *Clitocybe* sp., *Cortinarius* sp., *Lactarius torminosus* (Schaeff.) Gray, *L. turpis* (Weinm.) Fr., *Lepista nuda* (Bull.) Cooke, *Paxillus involutus* (Batsch) Fr., *Pholiota* sp., *Pleurotus ostreatus* (Jacq.) P. Kumm., *Russula vinosa* Lindblad, *Stropharia hornemannii* (Fr.) S. Lundell & Nannf., *Tricholoma equestre* (L.) P. Kumm., and *T. imbricatum* (Fr.) P. Kumm., and the flat hymenophore by *Coniophora puteana* (Schumacher.) P. Karst., *Dendrothele griseocana* (Bres.) Bourdot & Galzin, *Stereum rugosum* Pers., *Thelephora terrestris* Ehrh., and *Vesiculomyces citrinus* (Pers.) E. Hagstr.

2.2 Charge-to-mass quotient and charge of spores

For each sample, the mean charge-to-mass quotients for negatively and positively charged spores were determined and the mean positive charge of spore and the mean negative charge of spore were calculated as described in Saar (2013). Length and width of spores were taken equal to the mean values given by Niemelä (2008) or were computed by us as means of the minimum and maximum values given by Kalamees (1971b, 1972) and others (Corner 1968; Eriksson and Ryvarden 1975; Eriksson et al. 1984; Gilbertson and Hemmes 1997; Nakasone 2006; Sell 2008). The Pearson's correlation coefficients (r) were computed to see whether correlations between the magnitude of the spore charge-to-mass quotient and the spore

volume, and between the magnitude of the spore charge and the spore volume were present or not.

2.3 Hymenial emission rate of charged spores and charges

The hymenial emission rate of charged spores shows a number of charged spores released per second per cm² of hymenial surface area, *i.e.*, per unit area of outer surface (neglecting the internal hymenial structure). It was calculated using the numbers of positively charged spores and negatively charged spores released from the area of 0.44 cm² of the hymenial surface during the collection of spore sample. The hymenial emission rate of charges was computed multiplying the hymenial emission rate of charged spores by the number of elementary charges on the mean charged spore.

2.4 Variability and correlation in charges and hymenial emission rates

The variation coefficients (v) of both the charges and the emission rate were found. By that, as the classical estimator $v = 100(s/a)$ gives underestimated values in the case of the small set size (amount of samples in a species, n), the unbiased estimator using the small set correction proposed by Haldane (1955) was calculated of the form

$$v = 100(s/a) (1 + 1/4n), \quad (1)$$

where s is the standard deviation and a is the arithmetic average of the emission rates or charges in a set. The Pearson's correlation coefficient (r) was computed to see whether correlation between the charge magnitude and the hymenial emission rate was present or not.

2.5 Synchrony and difference in hymenial emission rates

To get preliminary data about the variation ranges, synchrony, and differences in the hymenial emission rates of charged spores, the repeated spore collections was carried out in a group of fruitbodies in *Fomes fomentarius* and *Ganoderma applanatum*; in *Fomitopsis pinicola*, the spore collections were carried out in different groups of fruitbodies at different times (Tables 1, 2). The Friedman rank test, Spearman's

rank-order correlation, and Student's test were used to analyze the data. In t tests, due to limited set size ($n \leq 6$), we considered $p = 0.10$ as significance level.

Due to a wide variation in the values of emission rate, we used the logarithmic transformation for emission rate. No transformation was used for charge-to-mass quotient and charges.

2.6 Fruitbody number on forested territory

For three fungal species involved in the present study on spore charges, empirical data on the seasonal dynamics of fruitbody numbers per hectare were available in the literature—for *Cantharellus cibarius* and *Paxillus involutus* in pine and pine-birch forests (Lõugas 1980) and for *Phellinus tremulae* in aspen stands (Tamm 2000). We computed the fruitbody numbers per hectare for *C. cibarius* and *P. involutus* in the peak period of the fruitbody production (September) and for *P. tremulae*, in stands 40 years old and older.

2.7 Area of hymenial surface on forested territory

The area of hymenial surface per hectare of forest was computed multiplying the number of fruitbodies growing on this unit area by the hymenial surface area of the mean fruitbody. The fruitbody's hymenial area was considered to have shape of an annulus with the outer diameter of 11.5 cm in *Paxillus involutus* and 6.5 cm in *Cantharellus cibarius* and with the inner diameter of 1.5 cm in both [the mean width of pileus and stipe according to Kalamees (1971b)]. In *Phellinus tremulae*, the fruitbody's hymenial area was considered to have shape of an ellipse with axes of 4 and 5 cm (Ülo Tamm, personal communication).

2.8 Territorial emission rate of charged spores and charges

The territorial emission rate of charged spores shows the number of charged spores released per second per hectare of forest. It was calculated multiplying the hymenial emission rate of charged spores by the area of hymenial surface per hectare of forest. The territorial emission rate of charges was computed by multiplying the territorial emission rate of charged spores and the number of charges on the mean charged spore.

2.9 Charge relaxation time

As described above, the freshly emitted basidiospores and pollen grains can carry high electric charges, which considerably exceed the steady-state charges of atmospheric aerosol particles. However, the atmospheric air is ceaselessly ionized and steadily contains negative and positive air ions. The highly charged basidiospores and pollen grains attract oppositely charged air ions, and thus, their charge diminishes or relaxes during time. Let us estimate the rate of such charge relaxation.

The diffusion charging processes of aerosol particles are described by Salm and Tamm (2011). If the initial charge of an aerosol particle considerably exceeds the steady-state charge, then we may take into account only the oppositely charged air ions. Let us consider a spherical aerosol particle with a high charge of ie , where e is the positive elementary charge and i is the number of elementary charges on a particle. In the case of negative charges, i is negative.

The strength of the electric field on the surface of the charged particle is

Table 1 Study setup in *Fomes fomentarius* and *Ganoderma applanatum* (for the repeated spore collections, carried out in a group of fruitbodies) and in *Fomitopsis pinicola* (for the spore collections, carried out in different groups of fruitbodies at different times)

Species	A series of spore collections				Number of fruitbodies studied simultaneously
	Number of collections	Number of spore samples per fruitbody	Duration of collection period	Time interval involved per series	
<i>Fomes fomentarius</i>	6	6	15–36 min	69 h	4
<i>Ganoderma applanatum</i>	4	4	45–60 min	50 h	3
<i>Fomitopsis pinicola</i>	4	1	50–168 min	179 h	6 (in three collections) and 4 (in one collection)

Table 2 Study subjects and results in *Fomes fomentarius* and *Ganoderma applanatum* (the repeated spore collections, carried out in a group of fruitbodies) and in *Fomitopsis pinicola* (the spore collections, carried out in different groups of fruitbodies at different times)

Species	Study subject	Results
<i>Fomes fomentarius</i>	Variation range of the fruitbody HER	The minimum range stayed within 1 order of magnitude (in fruitbody III, 116–715 spores $\text{cm}^{-2} \text{s}^{-1}$), the maximum range extended over 3 orders of magnitude (IV, 2–587 spores $\text{cm}^{-2} \text{s}^{-1}$)
<i>F. fomentarius</i>	Variation range of the group HER	Extended over 2 orders of magnitude [the group of fruitbodies I–IV, 19 spores $\text{cm}^{-2} \text{s}^{-1}$ (95 % confidence interval of 4–100 spores $\text{cm}^{-2} \text{s}^{-1}$) in period <i>b</i> to 517 (416–644) spores $\text{cm}^{-2} \text{s}^{-1}$ in period <i>d</i>]
<i>F. fomentarius</i>	Synchrony of dynamics of HER between fruitbodies	Absent in five pairs of fruitbodies (in I&II, I&III, I&IV, II&IV, and III&IV the Spearman's rank-order correlation coefficient $r_s = 0.2$ – 0.7 , number of time periods $n = 6$, $p = 0.1$) and present in one pair (II&III, $r_s = 0.943$, $n = 6$, $p = 0.02$)
<i>F. fomentarius</i>	Difference between fruitbodies in the mean fruitbody HER	Nonsignificant [the Friedman rank test statistic chi-square = 5.4 for four fruitbodies ($df = 3$), $p = 0.14$]
<i>F. fomentarius</i>	Difference between periods in the group HER	Significant [the Friedman rank test statistic chi-square = 13.6 for six time periods ($df = 5$), $p = 0.02$]
<i>Ganoderma applanatum</i>	Variation range of the fruitbody HER	Extended over 2 orders of magnitude in one fruitbody (II, 9–57 spores $\text{cm}^{-2} \text{s}^{-1}$) and over 3 orders in the rest of fruitbodies (I, 8–343; III, 8–296)
<i>G. applanatum</i>	Variation range of the group HER	Extended over 2 orders of magnitude [the group of fruitbodies I–III, 10 spores $\text{cm}^{-2} \text{s}^{-1}$ (95 % confidence interval of 7–15 spores $\text{cm}^{-2} \text{s}^{-1}$) in period <i>a</i> to 113 (42–299) spores $\text{cm}^{-2} \text{s}^{-1}$ in period <i>d</i>]
<i>G. applanatum</i>	Synchrony of dynamics of HER between fruitbodies	Absent in all pairs of fruitbodies (in I&II, I&III, II&III the Spearman's rank-order correlation coefficient $r_s = 0.0$ – 0.8 , number of time periods $n = 4$, $p = 0.1$)
<i>G. applanatum</i>	Difference between fruitbodies in the mean fruitbody HER	Nonsignificant [the Friedman rank test statistic chi-square = 1.5 for three fruitbodies ($df = 2$), $p = 0.47$]
<i>G. applanatum</i>	Difference between periods in the group HER	Nonsignificant [the Friedman rank test statistic chi-square = 5.4 for four periods ($df = 3$), $p = 0.14$]
<i>Fomitopsis pinicola</i>	Variation range of the group HER	Extended over 2 orders of magnitude [9 spores $\text{cm}^{-2} \text{s}^{-1}$ (95 % confidence interval of 4–21 spores $\text{cm}^{-2} \text{s}^{-1}$) in the group of four fruitbodies in period <i>h</i> to 23 (8–67) spores $\text{cm}^{-2} \text{s}^{-1}$ in period <i>e</i> in the group of six fruitbodies]
<i>Fomitopsis pinicola</i>	Difference between periods in the group HER	Nonsignificant [$t = -0.3 \dots + 1.4$; for four periods ($df = 10$ for periods where the groups of 4 and 6 fruitbodies were studied, and $df = 8$ for periods where the groups of 6 fruitbodies were studied), $p = 0.1$]

Marks. HER—hymenial emission rate of charged spores; I, II, ...—fruitbodies (see Figs. 1, 2); *a*, *b*, ...—spore collection periods (see Figs. 1, 2); the mean fruitbody HER—average hymenial emission rate of charged spores over all periods studied per fruitbody; the group HER—average hymenial emission rate of charged spores over all fruitbodies studied simultaneously per period

$$E = \frac{ie}{4\pi\epsilon_0 r_p^2} \quad (2)$$

where ϵ_0 is the electric constant and r_p is the radius of the particle.

The electric current density of oppositely charged air ions through the surface of the charged particle is

$$J^- = \sigma^- E = \frac{\sigma^- ie}{4\pi\epsilon_0 r_p^2}, \quad (3)$$

where σ^- is the polar conductivity of air due to the oppositely charged air ions.

The electric current strength through the entire surface of charged particle

$$I^- = 4\pi r_p^2 J^- = ie\sigma^-/\epsilon_0. \quad (4)$$

If we consider the charge number i as a continuous variable, then the current strength may be expressed through the derivative of i with respect to time t . The obtained current strength is equal to the current strength expressed in Eq. (4), and thus, we result in a simple differential equation and its solution

$$i = i_0 \exp\left(-\frac{t}{\tau}\right), \quad (5)$$

where i_0 is the initial charge number of a particle, and τ is the charge relaxation time,

$$\tau = \epsilon_0/\sigma^-. \quad (6)$$

The initial charge number diminishes about 2.7 times during a time interval of τ and 7.3 times during 2τ . The rate of charge relaxation does not depend on the size of particles. Equation (6) is derived also in the monograph (Chalmers 1967) with somewhat different context. If the initial charge is not considerably higher than steady-state charges, then the theory needs refinements (Salm and Tamm 2011).

3 Results

3.1 Spore charge and hymenial emission rate of charged spores

In total, 128 spore samples from 81 fruitbodies of 31 species were studied (Table 3). All these samples exhibited a majority of charged spores. The polarity distribution of charges in a sample was unipolar-negative or unipolar-positive, or bipolar. All samples,

originating from a certain species, displayed the same polarity distribution (Figs. 1, 2, 3). The absolute value of charges was in the range of orders of magnitude of 10–1,000 e (Table 4).

The hymenial emission rate of charged spores was in the range of orders of magnitude of 0.1–100 spores $\text{cm}^{-2} \text{s}^{-1}$ (Figs. 1, 2, 3; Table 5). In all bipolar species (except *Thelephora terrestris* and *Cantharellus cibarius*), both components of the charged spores had emission rates in this range. In *T. terrestris* and *C. cibarius*, the positive spores had emission rate in the order of magnitude of 0.001 spores $\text{cm}^{-2} \text{s}^{-1}$. The maximum found was 343 spores $\text{cm}^{-2} \text{s}^{-1}$ for positive spores and 715 spores $\text{cm}^{-2} \text{s}^{-1}$ for negative spores.

Variability of charge magnitudes was several times lower than that of the hymenial emission rates: v of charges 18 % and v of emission 75 % in *Fomes fomentarius*; 15 and 198 % in *Fomitopsis pinicola*; 26 and 118 % in *Ganoderma applanatum*; 23 and 123 % in *Lactarius turpis*. Correlation between the charge magnitude and the hymenial emission rate was absent ($r = 0.01$; set of 26 spore samples in *F. fomentarius* and $r = 0.03$; 28 samples in *F. pinicola*). Correlation between the magnitude of spore charge-to-mass quotient and the spore volume was absent ($r = -0.07$; set of 49 pairs listed in Table 4, $df = 47$, $p = 0.63$). Correlation between the magnitude of spore charge and the spore volume was significant ($r = 0.50$; set of 49 pairs listed in Table 4, $df = 47$, $p = 0.0002$, 95 % confidence level 0.26–0.69).

3.2 Synchrony and difference in hymenial emission rates

The hymenial emission rate of charged spores was characterized by constant change—this was shown by the series of repeated samples in *F. fomentarius* and *G. applanatum* (Figs. 1, 2). The fruitbodies, although studied simultaneously, showed uneven extents of the variation ranges of the hymenial emission rate of charged spores (Table 2). Dynamics of the hymenial emission rate were asynchronous in fruitbodies (Table 2). Differences between fruitbodies in the mean fruitbody hymenial emission rate were nonsignificant (Table 2). Differences between periods in the group hymenial emission rate were nonsignificant in *G. applanatum* and *F. pinicola*, but significant in *F. fomentarius* (Table 2).

Table 3 Study on the hymenial emission rate of charged spores in 31 species of Agaricomycetes: number of fruitbodies, time periods, spore samples, repeated collections and simultaneous collections per species

Species ^a	Number of			Number of repeated samplings per fruitbody	Number of simultaneous samplings per time period
	fruitbodies	time periods	spore samples		
<i>Fomes fomentarius</i>	4	8	26	8, 6, 6, and 6	4(6) (the same four fruitbodies in six periods)
<i>Fomitopsis pinicola</i>	26	8	28	2	6, 6, 6, 4, and 2(2)
<i>F. rosea</i>	4	1	4	non	4
<i>Ganoderma applanatum</i>	3	5	13	5, 4, and 4	3(4)
<i>Lactarius turpis</i>	8	3	10	2 and 2	6, 2, and 2(2)
<i>Paxillus involutus</i>	4	3	7	2, 2, and 2	3(2)
<i>Phellinus populicola</i>	4	3	6	3	4
<i>Clitocybe</i> sp.	2	1	2	non	2
<i>Coniophora puteana</i>	1	2	2	2	non
<i>Cortinarius</i> sp.	2	2	3	2	2
<i>Phellinus tremulae</i>	2	2	2	non	non
<i>Pholiota</i> sp.	1	2	2	2	non
<i>Stropharia hornemannii</i>	2	2	3	2	2
<i>Tricholoma imbricatum</i>	1	2	2	2	non
<i>Vesiculomyces citrinus</i>	1	2	2	2	non

^a The other 16 species were represented by one spore sample (Table 4)

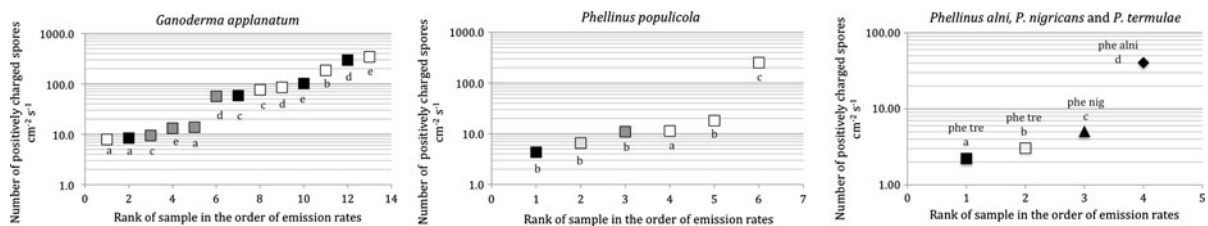


Fig. 1 Hymenial emission rate of charged spores in the spore samples where the polarity distribution of spore charges was unipolar-positive. Marks to indicate time and duration of spore collection and fruitbodies examined on the chart “*Ganoderma applanatum*”—Fruitbodies: white I, gray II, black III. Times: all samplings were performed in 1973; a sampling date 5 July, start time 19:08, duration 60 min; b 5 July, 23:10, 60 min; c 6 July, 21:45, 45 min; d 7 July, 10:00, 60 min; e 7 July, 19:50, 60 min.

“*Phellinus populicola*”—Fruitbodies: white I, light gray II, dark gray III, black IV. Times: all samplings were performed in 1973; a sampling date 9 July, start time 9:24, duration 7 h 6 min; b 25 June, 22:33, 9 h; c 30 September, 16:00, 2 h 55 min. “*Phellinus alni* etc.”—Fruitbodies: black I, white II. Time periods: all samplings were performed in 1973; a 31 May, 18:34, 3 h 46 min; b 31 May, 23:10, 11 h 40 min; c 5 Oct, 17:10, 1 h 50 min; d 8 Oct, 16:30, 2 h 30 min

3.3 Area of hymenial surface on forested territory. Territorial emission rate of charged spores and charges

The fungal fruitbodies of *Phellinus tremulae* occur on aspen (*Populus tremulae*) stems over 30 years old. The percentage of trees with fruitbodies increases as the stand

grows older (Table 6). The number of fruitbodies reaches its maximum in 75-year-old stands, corresponding to the hymenial area of about $10 \text{ m}^2 \text{ ha}^{-1}$ in predominantly aspen stands. In such stand and older by the hymenial emission rate and spore charges measured by us, emission of about 3×10^5 positively charged spores $\text{s}^{-1} \text{ ha}^{-1}$ and 3×10^7 e $\text{s}^{-1} \text{ ha}^{-1}$ occurred (Table 7).

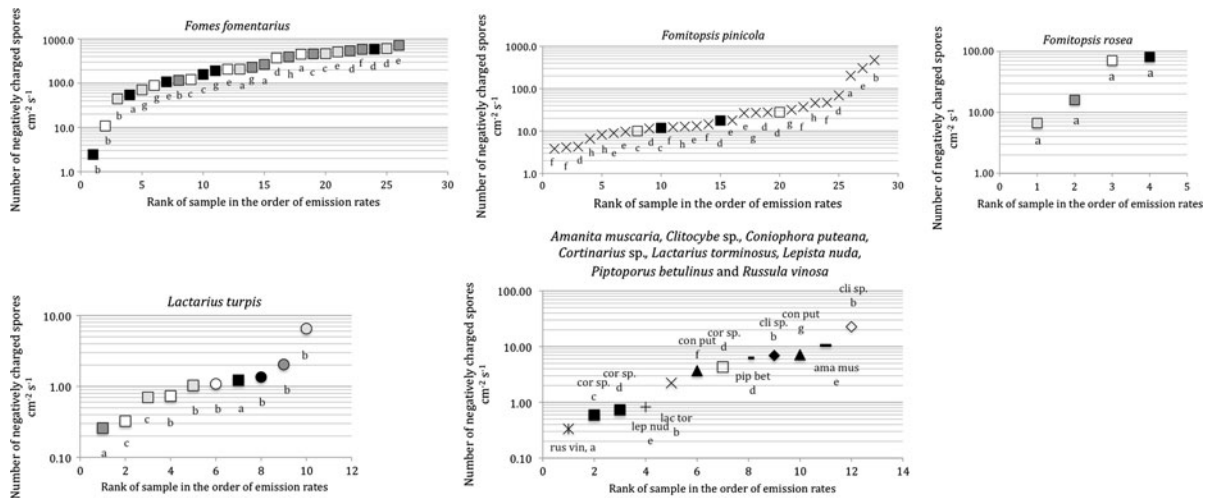


Fig. 2 Hymenial emission rate of charged spores in the spore samples where the polarity distribution of spore charges was unipolar-negative. Marks to indicate time and duration of spore collection and fruitbodies examined on the chart “*Fomes fomentarius*”—Fruitbodies: white I, light gray II, dark gray III, black IV. Times: all samplings were performed in 1973; a sampling date 1 June, start time 20:27, duration 36 min; b 1 June, 21:36, 20 min; c 2 June, 17:13, 29 min; d 2 June, 18:10, 20 min; e 2 June, 18:50, 15 min; f 2 June, 19:35, 25 min; g 4 June, 17:11, 30 min; h 4 June, 18:14, 45 min. “*Fomitopsis pinicola*”—Fruitbodies: black XVII, white XXI, X–26 different fruitbodies, each with a single sample. Times: samplings were performed in 1973 (a) and 1974 (b–h); a sampling date 21 May, start time 22:33, duration 50 min; b 2 June, 17:15, 65 min; c 3 June, start in the interval of 9:11–9:53, duration in the interval of 55–65 min; d 4 June, 8:42–9:16, 60 min; e 7 June, 9:27–9:49, 50–65 min; f 8 June, 17:57–18:50, 2–2 h 48 min; g 9 June,

9:34–9:44, 55 min; h 11 June, 18:10, 2 h. “*Fomitopsis rosea*”—Fruitbodies: white I, light gray II, dark gray III, black IV. Times: all samplings were performed simultaneously in 1973 on 9 July, start time 9:24, duration 7 h 6 min (a). “*Lactarius turpis*”—Fruitbodies: black square I, dark gray square II, light gray square III, white square IV, black ring V, dark gray ring VI, light gray ring VII, white ring VIII. Times: all samplings were performed in 1973; a sampling date 15 September, 9:00, 10 h 15 min; b 21 September, 18:00, 2 h; c 22 September, 17:45, 2 h. “*Amanita muscaria*, etc.”—Fruitbodies: black I, white II. Times: samplings were performed in 1973 (a–e) and 1978 (f, g); a 19 September 1973, 16:20, 3 h 30 min–2 h 40 min; b 30 September 1973, 16:20–16:30, 2 h 30 min–2 h 40 min; c 5 October 1973, 17:00, 2 h 10 min; d 6 October 1973, 16:55–17:15, 1 h 30 min–2 h; e 7 October 1973, 17:10–17:40, 1 h 10 min–1 h 40 min; f 15 September 1978, 8:55, 22 h 5 min; g 16 September 1978, 8:15, 23 h 5 min

Production of fruitbodies of *Paxillus involutus* and *Cantharellus cibarius* strongly varied in pine and pine-birch forests (Table 8). The *P. involutus* fruitbodies were most numerous in the paludified *Calluna* pine-birch forest. There the peak time of fruitbody production corresponded to the hymenial area of about $2 \text{ m}^2 \text{ ha}^{-1}$. By the hymenial emission rate and spore charges measured by us, emission of about 5×10^4 positively charged spores $\text{s}^{-1} \text{ ha}^{-1}$ and $6 \times 10^6 \text{ e s}^{-1} \text{ ha}^{-1}$, and 2×10^4 negatively charged spores $\text{s}^{-1} \text{ ha}^{-1}$ and $-3 \times 10^6 \text{ e s}^{-1} \text{ ha}^{-1}$ occurred (Table 9). Contrary to *P. involutus*, which was among dominant species in all forests studied, *C. cibarius* belonged to the dominants only in the lichen pine-birch forest. There the peak time of its fruitbody production corresponded to the hymenial area of about $5 \text{ m}^2 \text{ ha}^{-1}$. By the hymenial emission rate and spore charges measured by us, emission of about 500 positively charged spores $\text{s}^{-1} \text{ ha}^{-1}$ and $60,000 \text{ e s}^{-1}$

ha^{-1} , and 2×10^5 negatively charged spores $\text{s}^{-1} \text{ ha}^{-1}$ and $-6 \times 10^7 \text{ e s}^{-1} \text{ ha}^{-1}$ occurred.

In pine and pine-birch forests in a year of a quite poor yield of mushrooms, the group of edible fungi corresponded to the hymenial area of $11\text{--}12 \text{ m}^2 \text{ ha}^{-1}$ at the peak time of the fruitbody production (Table 8, the nonbog forests). In mature pine forests, in years of poor yield, the ratio of the number of inedible fruitbodies/the number of edible fruitbodies varies from 0.8 to 2.2 (Kalamees and Silver 1988). Basing on these data and assuming equality of the groups of edible and inedible fungi in a mean hymenial area of fruitbody, we got $20\text{--}42 \text{ m}^2 \text{ ha}^{-1}$ for an estimation of the area of the hymenial surface of mushrooms in mature pine and pine-birch forests in a year of a poor yield. In the eutrophic *Hepatica* boreo-nemoral spruce forest, at the peak time of fruitbody production of mushrooms, edible and inedible fungi altogether

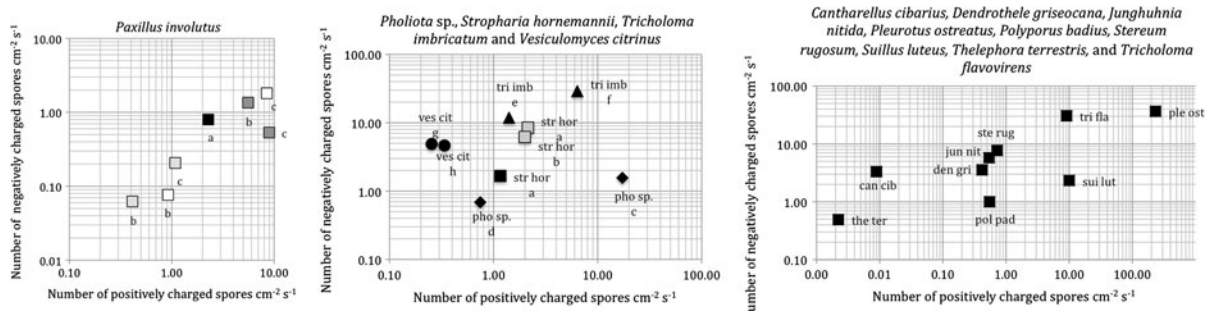


Fig. 3 Hymenial emission rate of charged spores in the spore samples where the polarity distribution of spore charges was bipolar. Marks to indicate time and duration of spore collection and fruitbodies examined on the chart “*Paxillus involutus*”—Fruitbodies: black I, dark gray II, light gray III, white IV. Times: all samplings were performed in 1973; a sampling date 23 September, 16:00, 3 h; b 9 October, 18:00, 14 h; c 10 October, 16:10, 3 h. “*Pholiota* sp., etc.”—Fruitbodies: the same marks mean the same fruitbody. Times: samplings were performed in 1973 (a–f) and 1978 (g, h); a sampling date 30 September 1973, sampling start 15:55, sampling duration 3 h; b 4 October 1973,

17:50, 1 h 30 min; c 5 October 1973, 16:30, 2 h 55 min; d 6 October 1973, 16:40, 2 h 25 min; e 7 October 1973, 16:35, 2 h 35 min; f 8 October 1973, 18:00, 1 h 30 min; g 19 September 1978, 10:00, 23 h; h 20 September 1978, 10:30, 7 h 45 min. “*Cantharellus cibarius*, etc.”—Fruitbodies: one fruitbody per species. Times: samples were performed in 1973 (a–d) and 1978 (e–g); a 17 Sept, 16:55, 2 h; b 5 October, 16:10, 3 h 15 min; c 8 October, 18:00, 1 h 30 min; d 9 October, 16:40, 3 h; e 16 September, 8:15, 23 h 5 min; f 17 September, 9:40, 24 h 20 min; g 18 September, 11:30, 22 h

corresponded to the hymenial area of about $1.1\text{--}1.6\text{ m}^2\text{ ha}^{-1}$ (our estimation according to 21 dominant species in Vooremaa in September 1970; Kalamees and Kollom 1971).

3.4 Charge relaxation time

Let us estimate the charge relaxation time in real atmospheric conditions near the ground level. Equation (6) contains the electric constant $\varepsilon_0 = 8.854 \times 10^{-12}\text{ F m}^{-1}$ and the polar conductivity of air σ^- . The polar conductivity of air can be estimated on the basis of the regular long-term air ion measurements carried out at the Tahkuse Observatory, Estonia. Tahkuse Observatory with coordinates $58^\circ 31' \text{N}$, $24^\circ 56' \text{E}$ is located in a sparsely populated rural region. The air was sucked into the mobility spectrometers through an opening in the south gable of the building at a height of about 5 m from the ground. A thoroughly analyzed measurement period lasted from September 1, 1993 to October 27, 1994 (Hõrrak et al. 2000). The average polar conductivity σ^- for this period equals to 6.18 fS m^{-1} . Taking into account this value of polar conductivity, the charge relaxation time can be calculated by means of Eq. (6) as $\tau = 1,430\text{ s}$. Thus, the initial charge number diminishes about 2.7 times during a time of 1,430 s.

4 Discussion

4.1 Presence of charges

Studying the primary electric charges of ballistic basidiospore, we did not found spore samples consisting of electrically neutral spores or having a majority of neutral spores. Such spore samples have not been reported in earlier studies (Buller 1909; Gregory 1957; Swinbank et al. 1964; Webster et al. 1988). Altogether more than 150 spore samples and 100 fruitbodies covering 43 species, 33 genera, 23–25 families, and 9 orders (Auriculariales plus those eight listed in “Materials and methods”) of Agaricomycetes and one species of Tremellomycetes (Basidiomycota) (Webster et al. 1988) have exhibited the presence of the electric charges on basidiospores. The charged spores were released by mature and healthy macroscopic fruitbodies (Gregory 1957; Swinbank et al. 1964; present study), small pieces of the macroscopic fruitbodies (Buller 1909; Webster et al. 1988), and a microscopic basidiomycetous fungus—a basidiomycete yeast (Webster et al. 1988). These results show, firstly, that the charged spores have been observed at different times within 80 years, at different places apart from each other up to thousands of kilometers, in different environmental conditions from forests to laboratories, and in the majority of orders of

Table 4 Magnitude of spore charge in 31 species of Agaricomycetes: computation on the base of spore charge-to-mass quotient (found out in natural forest conditions in Estonia) and spore sizes (taken from literature)

Species and polarity of spore charges	Charge-to-mass quotient (10 ^{−4} C kg ^{−1})				Sizes (μm)		Shape	Volume (μm ³)	Charge (e)			
	Mean	95 % confint	Stdev	Range	Length	Width			Source	Mean	95 % confint	Stdev
<i>Amanita muscaria</i> −	1.56	0.81–2.30	non	non	10	7.5	I	295	286	149–423	non	non
<i>Coniophora puteana</i> −	1.46	1.13–1.79	0.24	0.72–2.26	10.5	6.5	II	232	212	165–260	34	105–328
<i>Cantharellus cibarius</i> −	4.57	3.15–5.99	non	non	9	5.25	I	125	355	245–466	non	non
<i>C. cibarius</i> +	1.65	0.98–2.33	non	non	9	5.25	I	125	128	76–181	non	non
<i>Clitocybe</i> sp. <i>L</i> −	3.24	2.63–3.85	0.44	1.49–5.25	4.4	3.5	I	28	57	46–68	8	26–92
<i>Clitocybe</i> sp. <i>U</i> −	3.24	2.63–3.85	0.44	1.49–5.25	7.5	5.5	I	119	240	195–285	33	110–389
<i>Corinarius</i> sp. <i>L</i> −	2.32	1.95–2.70	0.33	0.90–3.85	7.5	4.5	I	80	115	97–134	17	45–191
<i>Corinarius</i> sp. <i>U</i> −	2.32	1.95–2.70	0.33	0.90–3.85	15	8	I	503	729	610–848	105	282–1,208
<i>Dendrothele griseocana</i> −	0.93	0.56–1.30	non	non	11	9	III	467	271	162–379	non	non
<i>D. griseocana</i> +	0.89	0.52–1.25	non	non	11	9	III	467	258	151–365	non	non
<i>Fomes fomentarius</i> −	5.78	5.38–6.18	1.04	2.65–8.94	17.8	5.4	IV	272	981	913–1,049	176	450–1,517
<i>Fomitopsis pinicola</i> −	6.09	5.77–6.42	0.89	3.14–11.00	7.6	3.9	IV	61	230	218–243	33	119–416
<i>Fomitopsis rosea</i> −	5.13	4.68–5.58	0.46	3.34–7.08	5.8	2.4	IV	26	84	77–91	8	55–116
<i>Ganoderma applanatum</i> +	2.18	1.87–2.48	0.56	0.92–4.62	8.2	5.7	IV	118	161	138–183	41	68–341
<i>Junghuhnia nitida</i> −	2.63	1.56–3.70	non	non	4.2	2.6	IV	22	37	22–52	non	non
<i>J. nitida</i> +	1.53	0.89–2.17	non	non	4.2	2.6	IV	22	21	12–30	non	non
<i>Lactarius turpis</i> −	2.66	2.30–3.03	0.59	0.87–4.87	8	5.75	I	138	230	199–262	51	75–421
<i>Lactarius torminosus</i> −	0.74	0.38–1.10	non	non	9	7	I	231	107	55–158	non	non
<i>Lepista nuda</i> −	1.88	0.86–2.90	non	non	7	4.75	I	83	97	44–150	non	non
<i>Paxillus involutus</i> −	1.68	1.32–2.04	0.48	0.48–3.48	9	5.5	I	143	149	118–181	43	43–310
<i>P. involutus</i> +	1.53	1.08–1.97	0.61	0.52–3.87	9	5.5	I	143	136	96–176	54	46–344
<i>Phellinus alni</i> +	2.12	1.10–3.14	non	non	5.94	5.11	VIII	81	107	56–159	non	non
<i>Phellinus nigricans</i> +	2.78	1.41–4.15	non	non	6.55	5.86	VIII	118	204	104–305	non	non
<i>Phellinus populicola</i> +	3.68	2.69–4.68	1.25	1.15–6.60	5.58	4.76	VIII	66	152	120–184	52	48–273
<i>Phellinus tremulae</i> +	4.32	3.15–5.48	0.84	2.23–6.26	4.99	4.08	VIII	43	117	86–149	23	61–170
<i>Pholiota</i> sp. <i>L</i> −	1.65	1.56–1.74	0.06	0.75–2.55	5.75	3.5	I	37	38	36–40	1	17–59
<i>Pholiota</i> sp. <i>L</i> +	2.03	1.66–2.39	0.26	0.84–3.27	5.75	3.5	I	37	47	38–55	6	19–75
<i>Pholiota</i> sp. <i>U</i> −	1.65	1.56–1.74	0.06	0.75–2.55	8.5	5.6	I	140	144	136–151	6	65–222
<i>Pholiota</i> sp. <i>U</i> +	2.03	1.66–2.39	0.26	0.84–3.27	8.5	5.6	I	140	176	145–208	23	73–285
<i>Piptoporus betulinus</i> −	7.32	3.82–10.82	non	non	4.8	1.6	IV	10	44	23–65	non	non

Table 4 continued

Species and polarity of spore charges	Charge-to-mass quotient (10^{-4} C kg $^{-1}$)				Sizes (μm)			Shape	Volume (μm^3)	Charge (e)			
	Mean	95 % confint	Stdev	Range	Length	Width	Source			Mean	95 % confint	Stdev	Range
<i>Pleurotus ostreatus</i> –	3.12	1.60–4.64	non	non	9.5	3.5	I	C	91	178	91–265	non	non
<i>P. ostreatus</i> +	2.77	1.44–4.10	non	non	9.5	3.5	I	C	91	158	82–234	non	non
<i>Polyporus badius</i> –	1.84	0.90–2.78	non	non	7.8	3.6	IV	E	53	61	30–92	non	non
<i>P. badius</i> +	1.64	0.75–2.52	non	non	7.8	3.6	IV	E	53	54	25–83	non	non
<i>Russula vinosa</i> –	1.89	1.16–2.62	non	non	9.5	7.5	I	O	250	295	181–409	non	non
<i>Stropharia hornemannii</i> –	1.50	0.52–2.48	0.87	0.48–3.76	12	6.75	I	E	286	269	93–444	155	85–672
<i>S. hornemannii</i> +	1.03	0.70–1.36	0.29	0.43–2.08	12	6.75	I	E	286	183	124–243	52	77–372
<i>Stereum rugosum</i> –	2.17	1.19–3.15	non	non	9.5	3.75	V	C	105	142	78–206	non	non
<i>S. rugosum</i> +	1.39	0.74–2.04	non	non	9.5	3.75	V	C	105	91	48–134	non	non
<i>Suillus luteus</i> –	1.70	1.03–2.36	non	non	9	3.5	I	E	58	61	37–85	non	non
<i>S. luteus</i> +	1.32	0.84–1.81	non	non	9	3.5	I	E	58	48	30–65	non	non
<i>Thelephora terrestris</i> –	1.96	1.33–2.59	non	non	10	7.5	VI	E	295	360	245–476	non	non
<i>T. terrestris</i> +	11.44	4.68–18.20	non	non	10	7.5	VI	E	295	2,103	860–3,346	non	non
<i>Tricholoma equestre</i> –	1.74	0.89–2.59	non	non	6.5	4.5	I	E	69	75	38–111	non	non
<i>T. equestre</i> +	1.40	0.71–2.10	non	non	6.5	4.5	I	E	69	60	30–90	non	non
<i>Tricholoma imbricatum</i> –	2.24	2.05–2.42	0.13	1.09–3.46	6.5	4.5	I	E	69	96	88–104	6	47–149
<i>T. imbricatum</i> +	1.77	1.73–1.81	0.03	0.87–2.71	6.5	4.5	I	E	69	76	74–78	1	37–117
<i>Vesiculomyces citrinum</i> –	1.83	1.40–2.26	0.31	1.10–2.98	4.5	4.5	VII	E	48	55	42–67	9	33–89
<i>V. citrinum</i> +	0.99	0.88–1.10	0.08	0.56–1.53	4.5	4.5	VII	E	48	29	26–33	2	17–46

Marks: +positive polarity, –negative polarity, L—a species with the smallest spores in a genus in Estonia (*Clitocybe cerussata* in *Clitocybe*, *Cortinarius glaucopus* in *Cortinarius*, *Pholiota adiposa* in *Pholiota*), U—a species with the biggest spores (*Clitocybe geotropa*, *Cortinarius collinitus*, *Pholiota aurivella*), E—ellipsoid, C—cylinder, O—ovoid, mean—the arithmetic average of a single sample or of the set of all samples representing a species, non—absent (one spore sample per species), 95 % confint—the 95 % confidence interval of mean, stdev—standard deviation, range—interval from the lower border of the 95 % confidence interval of the smallest value in a setup to the upper border of the highest value, I—Kalamies (1972), II—Gilbertson and Hemmes (1997), III—Nakasone (2006), IV—Niemelä (2008), V—Eriksson et al. (1984), VI—Comer (1968), VII—Eriksson and Ryvarden (1975), VIII—Sell (2008)

Table 5 Hymenial emission rate of charged spores: statistics of sets of several ($n > 2$) spore samples in 9 species of Agaricomycetes

Species and polarity of spore charges	Hymenial emission rate (spores $\text{cm}^{-2} \text{s}^{-1}$)		
	Geometric average		Range
	Average	95 % confidence interval	
<i>Cortinarius</i> sp. –	1.2	0.0–4.7	0.6–4.3
<i>Fomes fomentarius</i> –	177	175–178	2.4–715
<i>Fomitopsis pinicola</i> –	21	20–23	3.8–471
<i>Fomitopsis rosea</i> –	28	26–30	6.7–81
<i>Ganoderma applanatum</i> +	46	44–48	7.9–343
<i>Lactarius turpis</i> –	1.0	0.0–2.8	0.3–6.5
<i>Paxillus involutus</i> – & +	2.8	0.3–5.2	0.5–10.4
<i>Phellinus populicola</i> +	16	13–19	4.3–251
<i>Stropharia hornemannii</i> – & +	6.3	4.1–8.5	2.8–10.6

Remarks. A set consisted of all samples representing a species, for the number of samples see Table 3. All the samples in a set had the same polarity distribution of charges, unipolar-positive (+) or unipolar-negative (–), or bipolar (– & +)

Agaricomycetes. The results show, secondly, that the charged spores occur in different classes of basidiomycetous fungi and that hymenium is not a precondition for the presence of the charges on basidiospores by their release into the air. Considering both circumstances, we concluded that the primary electric charges occur on basidiospores in all ballistosporic fungi of the Basidiomycota.

Table 6 Area of hymenial surface of *Phellinus tremulae* on forested territory in Estonia: estimation based on the literary data of numbers of trees in aspen stands and fruitbodies, and on the area of hymenial surface of a mean fruitbody (15.7 cm^2)

Data for K were taken from (Tamm 2000), for P from (Krigul 1969), and for R (Tamm 2000)

Stand age (years)	Tree number per ha, P	Relative amount of trees with fruitbodies, K	Fruitbody number per tree, R	Fruitbody number per ha, $P \times K \times R$	Area of hymenial surface per ha (m^2)
40	1,000	0.1	5	500	0.785
	1,200	0.1	5	600	0.942
55	750	0.6	7.6	3,420	5.37
	900	0.6	7.6	4,104	6.44
75	530	0.9	11.5	5,486	8.61
	700	0.9	11.5	7,245	11.37
>90	470	0.92	11.9	5,146	8.08
	600	0.92	11.9	6,569	10.31

4.2 Charge-to-mass quotient and charge of spore

Our results in spore charge-to-mass quotient and in charges accorded with the measurements made in basidiospores earlier. The ranges of absolute values of these two characteristics found by Swinbank et al. (1964) and Webster et al. (1988)— $(0.09 \div 13) \times 10^{-4} \text{C kg}^{-1}$ and $7 \div 6,710 \text{ e}$ [originally $(0.12 \div 107.50) \times 10^{-17} \text{C}$]—are wider than the ranges of our results and overlap ours entirely. All types of polarity distributions—the unipolar-positive, unipolar-negative, and bipolar—occur in charges of basidiospores that was seen by Buller (1909) and Gregory (1957) and by us. Earlier results show the absence of intraspecies variation in the polarity distribution in four species: *Agaricus campestris* and *Polyporus squamosus*, due to identical results of Buller (1909) and Gregory (1957); *Ganoderma applanatum* (Gregory 1957) and *Serpula lacrymans* (Swinbank et al. 1964). This coincides in our results that showed constancy in the polarity distribution in 15 species (listed in Table 3).

The main shortcoming of our study concerns *Cantharellus cibarinus* and *Thelephora terrestris*. In these species, relative importance of one unipolar part was extremely small (0.3–0.4 % of all charged spores in a spore sample), compared with the other bipolar species studied by us (5–48 %). In *T. terrestris*, the magnitude of mean charge of the positive spores was extremely big (2,103 e), compared with other species studied by us (21–981 e). We were backed on single spore samples. More samples should be examined.

Earlier and our results of the constancy in the polarity distribution concern 18 species covering 12 families and five orders of Agaricomycetes. In seven

Table 7 Territorial emission rate of charged spores and charges in *Phellinus tremulae* in aspen stands in Estonia: estimation based on the empirical data of hymenial emission

rate of spores and charges of spores (mean 117 e, 95 % confidence interval 86–149 e, range 61–170 e)

Age of stand (years)	Territorial emission rate of			
	Spores (10 ³ spores ha ⁻¹ s ⁻¹)	Charges (10 ⁶ e ha ⁻¹ s ⁻¹)		
		Mean	95 % conf int	Range
Hymenial emission rate of 3.04 charged spores cm ⁻² s ^{-1a}				
40	24	2.79	2.05–3.56	1.46–4.06
55	163	19.1	14.0–24.3	10.0–27.8
75	262	30.6	22.5–39.0	16.0–44.5
>90	246	28.7	21.1–36.6	15.0–41.8
40	29	3.35	2.46–4.27	1.75–4.87
55	196	22.9	16.8–29.2	11.9–33.3
75	346	40.4	29.7–51.5	21.1–58.8
>90	313	36.7	27.0–46.7	19.1–53.3
Hymenial emission rate of 752 charged spores cm ⁻² s ^{-1a}				
40	5,903	691	507–881	361–1,004
55	40,383	4,725	3,463–6,011	2,474–6,877
75	64,748	7,575	5,566–9,647	3,958–11,008
>90	60,762	7,109	5,220–9,054	3,711–10,340
40	7,084	829	609–1,056	433–1,205
55	48,429	5,666	4,156–7,223	2,944–8,237
75	85,503	10,004	7,347–12,740	5,220–14,545
>90	77,532	9,071	6,679–11,552	4,723–13,185

^a The value of 3.04 was found by us, 752 was taken from (Parmasto 1981) considering all released spores as charged ones

species, the spore sample originated from different fruitbodies and from 2–3 geographical sites and years. Based on this phylogenetically diverse set of species and the spatiotemporally diverse sets of spore samples per species, we conclude that, in basidiomycetous fungi, the polarity distribution of the primary electric charges of ballistosporic basidiospores is species-specific.

Factors responsible for the magnitude of spore charge, as well as the charge formation process itself are not known (Webster et al. 1988). Our correlation analyses showed that the charge magnitude does not depend on the sporulation intensity of fruitbody. The big charges tend to be on larger spores, and the smaller charges on smaller spores. The charge magnitude could partially (25 % of it) be explained by spore size (volume) or by something, which correlates with it. Studies of the spore discharge mechanism in the Basidiomycota revealed that large spores tend to produce larger Buller's drops and small spores

produce smaller drops (Stolze-Rybczynski et al. 2009). Correlation between area of the hilum (the place of spore insertion on the sterigma) and spore size has not been reported, but it is logical to suppose a positive correlation between them. These results support the hypotheses of endogenous origin of the primary electrostatic charges of ballistosporic basidiospores reported in (Saar 2013).

4.3 Magnitude of the hymenial emission rate of charged spores

As the hymenial emission rate of charged spores has not been reported earlier, we had to evaluate our results using data on the spore production (Table 10). The data of production include both charged and noncharged spores. Consideration of noncharged spores could not give much higher rates than the rates of charged spores, because the relative amount of noncharged spores is quite low (in our spore samples,

Table 8 Area of hymenial surface of *Paxillus involutus* and *Cantharellus cibarius* and of the group of species of dominant edible fungi in pine and pine-birch forests in North Estonia in

the peak period of the production of fruitbodies: an estimation based on the empirical data of number of fruitbodies in Lahemaa National Park in 1975, in a year of quite poor yield

Species or group of species	Fruitbody number per ha			Area of hymenial surface per ha (m ²)		
	Sept I	Sept II	Sept III	Sept I	Sept II	Sept III
Bog pine forest, Oruveski						
<i>P. involutus</i>	24	19	25	0.24	0.20	0.25
Dominants ^a	1,143	929	1,186	4.7	3.8	4.8
Paludified <i>Calluna</i> pure pine forest, Oruveski						
<i>P. involutus</i>	75	50	92	0.78	0.51	0.95
Dominants ^b	2,199	1,446	2,693	8.9	5.9	10.9
Paludified <i>Calluna</i> pine-birch forest, Käsmu						
<i>P. involutus</i>	197	175	149	2.02	1.79	1.53
Dominants ^c	2,247	1,992	1,702	9.6	8.5	7.3
Lichen pine-birch forest, Oruveski						
<i>C. cibarius</i>	1,025	1,616	732	3.2	5.1	2.3
<i>P. involutus</i>	50	79	36	0.52	0.81	0.37
Dominants ^d	2,008	3,164	1,434	7.7	12.1	5.4
<i>Calluna</i> pine-birch forest, Käsmu						
<i>P. involutus</i>	60	83	44	0.62	0.85	0.45
Dominants ^e	1,743	2,398	1,278	8.3	11.4	6.0

Remarks. Numbers of fruitbodies—according to the data in (Lõugas 1980). Sept I, II, III—at the end of the first, second, and third 10-day period. Area of the hymenial surface of fruitbody was computed using mean sizes of fruitbodies found according to size variation ranges given by Kalamees (1971b, 1972); 31.4 cm² in *C. cibarius* and 102.1 cm² in *P. involutus*

Dominants (ordered according to the number of fruitbodies, the most yielder species first)—^a *Lactarius rufus* (Scop.) Fr., *Russula emetica* (Schaeff.) Pers., *Lactarius helvus* (Fr.) Fr., *Rozites caperatus* (Pers.) P. Karst., and *Paxillus involutus* (Batsch) Fr.; ^b *Lactarius rufus*, *Paxillus involutus*, *Russula decolorans* (Fr.) Fr., *R. emetica*, and *R. paludosa* Britzelm.; ^c *Lactarius rufus*, *Paxillus involutus*, *Leccinum aurantiacum* (Bull.) Gray, *L. scabrum* (Bull.) Gray, *Tricholomopsis rutilans* (Schaeff.) Singer, and *Russula fragilis* var. *fragilis* Fr.; ^d *Cantharellus cibarius* Fr., *Lactarius rufus* (Scop.) Fr., *Suillus bovinus* (Pers.) Roussel, *Paxillus involutus*, *Sarcodon imbricatus* (L.) P. Karst., *Leccinum aurantiacum*, and *Suillus variegatus* (Sw.) Kuntze.; ^e *Rozites caperatus*, *Lactarius rufus*, *Suillus variegatus*, *Paxillus involutus*, *Boletus edulis* Bull., and *Russula aeruginea* Fr

it was mostly 0–10 % and rarely 30–40 % of all spores). In *F. fomentarius*, *F. pinicola*, *G. applanatum*, and *Phellinus populicola*, the range of earlier data overlaps our rates partially, their highest rates being 2- to 3-fold greater than our highest rate. In *Phellinus alni*, *P. nigricans*, *P. tremulae*, and *Piptoporus betulinus*, the earlier data contrast our rates, being 28- to 1,722-fold greater. These differences might be explained by the temporal scale of the studies and by the inter-fruitbodies variation in productivity. The earlier studies focused on 24-h spore samples collected across a sporulation period (Parmasto 1981) or a year (Kadowaki et al. 2010) or many successive days or months (Meyer 1936; Buchwald 1938; Rockett and Kramer 1974), while we focused on short time (tens of minutes) spore collections in a random day or some random days.

4.4 Variation and fluctuation in the hymenial emission rate of charged spores

Fluctuation of the hymenial emission rate of charged spores and large variation ranges of this rate in a *Fomes fomentarius* fruitbody—these our results accord with earlier observations of spore production (Rockett and Kramer 1974; Votintseva 2005). Absence of synchrony between *Fomes fomentarius* fruitbodies in the hymenial emission rate, which was observed by us, coincides with the earlier observations on spore production (Votintseva 2005). High variability of the hymenial emission rate of charged spores in a *Ganoderma applanatum* fruitbody accords with earlier observations on spore production (Haard and Kramer 1970; Kadowaki et al. 2010). Asynchronous spore release in *G. applanatum* fruitbodies, which was

Table 9 Territorial emission rate of charged spores and charges in *Paxillus involutus* and *Cantharellus cibarius* in pine and pine-birch forests in North Estonia: estimation based on empirical data of fruitbody numbers, and of charge magnitude and hymenial emission rate of spores for negative and positive components

Forest, site	Time	Territorial hymenial rate of					
		negative spores (10 ⁴ spores ha ⁻¹ s ⁻¹)	negative charges (10 ⁴ e ha ⁻¹ s ⁻¹)		positive spores (10 ⁴ spores ha ⁻¹ s ⁻¹)	positive charges (10 ⁴ e ha ⁻¹ s ⁻¹)	
			Mean	95 % conf int		Mean	95 % conf int
<i>Paxillus involutus</i>							
Bog pine forest, Oruveski							
	Sept I	0.25	37	29–45	0.56	77	54–99
	Sept II	0.21	31	24–37	0.47	64	45–83
	Sept III	0.26	38	30–47	0.59	80	56–103
Paludified <i>Calluna</i> pure pine forest, Oruveski							
	Sept I	0.80	120	95–145	1.83	249	176–323
	Sept II	0.53	78	62–95	1.20	163	115–211
	Sept III	0.98	146	115–177	2.23	304	214–393
Paludified <i>Calluna</i> pine-birch forest, Käsmu							
	Sept I	2.08	310	246–377	4.75	646	456–835
	Sept II	1.84	275	218–334	4.21	572	404–740
	Sept III	1.58	235	186–285	3.60	489	345–633
Lichen pine-birch forest, Oruveski							
	Sept I	0.54	80	63–97	1.22	166	117–215
	Sept II	0.83	124	98–151	1.90	259	183–335
	Sept III	0.38	57	45–69	0.87	118	83–153
<i>Calluna</i> pine-birch forest, Käsmu							
	Sept I	0.64	95	75–116	1.46	166	140–256
	Sept II	0.88	130	103–158	2.00	259	192–352
	Sept III	0.46	69	55–84	1.06	118	102–186
<i>Cantharellus cibarius</i>							
Lichen pine-birch forest, Oruveski							
	Sept I	10.62	3,772	2,603–4,951	0.03	3.7	2.2–5.2
	Sept II	16.93	6,011	4,148–7,890	0.05	5.9	3.5–8.3
	Sept III	7.64	2,711	1,871–3,558	0.02	2.6	1.6–3.7

Remarks. Hymenial emission rate of spores was taken equal to 1.03 negative and 2.35 positive spores per cm^2 per second in *P. involutus* (geometric mean of seven spore samples, Fig. 3), and 3.32 negative and 0.009 positive spores per cm^2 per second in *C. cibarius* (single sample, Fig. 3). For charges, look Table 4 and for territorial hymenial area, Table 8

observed by us, accords with earlier observations (Kadowaki et al. 2010). Altogether these data exhibit that fruitbodies of these polypores release the charged spores in fluctuating mode, independently from each other, and at the hymenial emission rate varying very largely within a day.

The most interesting result in the group hymenial emission rate of charged spores concerns the significant difference between time periods in *F. fomentarius*. This

shows that—despite asynchronous dynamics of the hymenial emission rate in fruitbodies—the group hymenial emission rate fluctuates significantly within a 24-h period. The fluctuations onto the highest level seem to be possible. To find the probability of occurrence of the situations when all fruitbodies release spore at near-maximum intensity, the repeated simultaneous measurements of the hymenial emission rate should be carried out using short-term (<20 min) periods.

Table 10 The earlier data of spore production expressed in the units of spores per s per cm² of hymenial surface

Species	Spore production		Number of fruiting bodies	Author
	Daily mean	Hourly mean		
<i>Fomes fomentarius</i>	903	–	1	Meyer (1936)
<i>F. fomentarius</i>	1,609	–	1	Buchwald (1938)
<i>F. fomentarius</i>	36	0.4–105	?	Lebkova (1972)
<i>F. fomentarius</i>	486 (914)	–	4	Parmasto (1981)
<i>Fomitopsis pinicola</i>	1.3	0.4–66	?	Lebkova (1972)
<i>F. pinicola</i>	127 (752)	–	4	Parmasto (1981)
<i>Ganoderma applanatum</i>	141–499	–	30	Kadowaki et al. (2010)
<i>Phellinus alni</i>	220 (1,100)	–	5	Parmasto (1981)
<i>Phellinus nigricans</i>	93 (370)	–	3	Parmasto (1981)
<i>Phellinus populicola</i>	150 (718)	–	4	Parmasto (1981)
<i>Phellinus tremulae</i>	185 (752)	–	7	Parmasto (1981)
<i>Piptoporus betulinus</i>	1,105	1,034–8,611	1	Rockett and Kramer (1974)

Parmasto (1981) gives the daily mean at average and at maximum, while Kadowaki et al. (2010) give the daily mean at minimum and at maximum. All these data but those of Lebkova (1972) represent the days of strong or moderate emission (“a 24-h period when spore production was near maximum,” Rockett and Kramer 1974; days “when the fruitbody produced more than 1×10^7 spores per 24 h,” Parmasto 1981; “weak seasonality in spore release,” Kadowaki et al. 2010). Lebkova’s data represent four consecutive 24-h periods in the II half of June, in the time when the strongest emission is over

4.5 Upper limit for the maximum hymenial emission rate of charged spores

To estimate contribution of basidiospores to the physicochemical processes of the atmosphere, one must know the upper limit for the total amount of spores released into a unit space in a time unit. To estimate this limit for a forest, one must know many factors, including the maximum hymenial emission rate of spores for every species inhabiting the forest. Values of hymenial emission rate are reported for species with poroid hymenophores, for polypores with narrow pores (listed in 4.3). Two of the highest values are 1,100 and 914 spores cm⁻² s⁻¹. Using these data, it is possible to estimate the upper limit for the maximum hymenial emission rate in fruitbodies with both lamellate and flat hymenophore. The maximum hymenial emission rate depends on the potential of the hymenium to produce spores and on the ratio (area of hymenium):(area of fruitbody undersurface). In poroid fruitbodies with narrow pores, this ratio is threefold greater than in lamellate fruitbodies, and 45-fold greater than in flat fruitbodies [approximation according to the data of Fischer and Money (2009)]. So, the upper limit is $914:3 = 305$ spores cm⁻² s⁻¹ to $1,100:3 = 367$ spores cm⁻² s⁻¹ in the group of lamellate fruitbodies, and

$914:45 = 20$ to $1,100:45 = 24$ spores cm⁻² s⁻¹ in the group of fruitbodies with flat hymenophore.

These theoretical upper limits are greater than the maximum values in our experimental data: 20–24 spores cm⁻² s⁻¹ (upper limit) versus 8.4 spores cm⁻² s⁻¹ (*Stereum rugosum*) in the group of fruitbodies with flat hymenophore, 305–367 spores cm⁻² s⁻¹ versus 269 spores cm⁻² s⁻¹ (*Pleurotus ostreatus*) in the group of fruitbodies with lamellate hymenophore, 914–1,100 spores cm⁻² s⁻¹ versus 715 spores cm⁻² s⁻¹ (*Fomes fomentarius*) in the group of fruitbodies with poroid hymenophore. Despite that, our experimental results showed that the spore production potential of hymenium similar to that in *Phellinus alni* or *F. fomentarius* may occur in the groups of lamellate hymenophore (in *P. ostreatus*, for example) and flat hymenophore (*S. rugosum*).

This estimation was carried out on the assumption that the spore production potential of the hymenium is similar to that in *Fomes fomentarius* and *Phellinus alni*. We overlooked the diversities of composition of the hymenium in Agaricomycetes, arrangement of configuration of hymenophore within each hymenophore configuration group of fruitbodies, life strategies of fungi, and environmental factors. Due to these simplifications, our estimate is very rough. But, it

might be acceptable in preliminary studies of contribution of the primary electric charges of basidiospores to the physicochemical processes of the atmosphere.

4.6 Number of fruitbodies: number of spore sources

The composition of species and productivity (both numbers of fruitbodies and biomass) of mushrooms strongly vary from year to year within the same forest stand (Kalamees and Silver 1988; Krastina 2000). The study Lõugas (1980) represents, according to an empirical estimation of the author, a year of a quite poor production, and the study Kalamees and Kollom (1971) represents a normal year production. Therefore, the numbers of fruitbodies per hectare were not overestimated in the present study.

While we computed territorial emission rate, all the fruitbodies were considered as the spore sources. But not always all fruitbodies do sporulate. The relative amount of nonsporulating fruitbodies varies through the season. In the mushrooms, this amount could be great (even equal to 100 %) during a few days at the beginning and at the end of season, and it is small (even equal to 0 %) during the remaining time of the season. Here, we were supported by the information on the development, growth, and sporulation of fruitbodies given by Haard and Kramer (1970), Kalamees (1971a), and Moore et al. (2008). Consequently, we did not overestimate the number of spore sources nor the territorial hymenial area in *Cantharellus cibarius*, *Paxillus involutus* and dominant groups in the peak time of the seasonal dynamics of fruitbody production, because it was reasonable for this time to consider all fruitbodies as spore sources. In the wood-inhabiting fungi, bias between the number of fruitbodies and the number of spore sources could occur if the seasonal dynamics of sporulation depends on the age of fruitbodies. This dependence is known in *Fomes fomentarius* and *Fomitopsis pinicola* (Votintseva 2005). A *P. tremulae* fruitbody sporulates from spring to autumn, irregularly performing some-day-long and some-week-long interruptions (Tamm 2000). Therefore, it is obvious all fruitbodies in a forest stand do not sporulate simultaneously. Our results of spore sources and of the territorial hymenial area in *Phellinus tremulae* should be considered as the theoretical maxima.

4.7 Territorial emission rate of charged spores

Our results on the territorial emission rate of charged *Phellinus tremulae* spores in aspen stand represented a weak sporulation in all fruitbodies. In the case of the upper limit of the hymenial emission ($752 \text{ spores cm}^{-2} \text{ s}^{-1}$; Parmasto 1981) in old aspen stands ($S_{\text{forest}} = 11.4 \text{ m}^2 \text{ ha}^{-1}$), the territorial emission rate of charged *Phellinus tremulae* spores should correspond to the value of 8.5×10^7 positively charged spores $\text{ha}^{-1} \text{ s}^{-1}$.

In *Cantharellus cibarius* and *Paxillus involutus*, our results represented a weak sporulation in a year of quite poor fruitbody production. The upper limits of the territorial emission rate (according to $367 \text{ spores cm}^{-2} \text{ s}^{-1}$) in such year should be 5×10^4 positively and 1.9×10^7 negatively charged spores $\text{ha}^{-1} \text{ s}^{-1}$ in *C. cibarius* ($S_{\text{forest}} = 5.1 \text{ m}^2 \text{ ha}^{-1}$), and 5×10^6 positively and 2×10^6 negatively charged spores $\text{ha}^{-1} \text{ s}^{-1}$ in *P. involutus* ($2.0 \text{ m}^2 \text{ ha}^{-1}$) at most densely populated areas.

In a year of normal fruitbody production in the boreo-nemoral spruce forest, the group of dominant litter-inhabiting species with lamellate fruitbodies (edible and inedible fruitbodies together) should emit up to $(367 \text{ spores cm}^{-2} \text{ s}^{-1}) \times (1.6 \text{ m}^2 \text{ ha}^{-1}) = 5.9 \times 10^6$ charged spores $\text{ha}^{-1} \text{ s}^{-1}$. In a year of quite poor fruitbody production in the lichen pine-birch forest, the fruitbodies of dominant litter-inhabiting species (edible and inedible fruitbodies together) should emit up to $(367 \text{ spores cm}^{-2} \text{ s}^{-1}) \times (12.8 \text{ m}^2 \text{ ha}^{-1} + 12.8 \text{ m}^2 \text{ ha}^{-1}) = 9.4 \times 10^7$ charged spores $\text{ha}^{-1} \text{ s}^{-1}$. These results show that tenfold differences between forests occur in territorial emission rates of charged spores of mushrooms.

At present, there are many gaps in our knowledge to consider all basidiomycetes. The number of fruitbodies and the area of hymenial surface in dominant wood-inhabiting species should be studied. Only after that, we could estimate the order of magnitude of the total number of charged spores and charges emitted from a unit area of forested territory in a time unit.

4.8 Relaxation time

The estimated above value of the charge relaxation time 1,430 s means that highly charged spores can spread over a considerably area depending on the wind velocity. Formerly, Bowker and Crenshaw (2003)

published somewhat similar analysis of charge relaxation time as in present article, but they found an estimation of 440 s for the time. The origin of such a short time came of the overestimated value of air conductivity. In addition, they considered total conductivity instead of polar conductivity.

5 Conclusion

Extensive information about airborne spores and about spore release had been collected in former publications in the field of aerobiology. However, the knowledge on electrostatic charges released by basidiospores into air was insufficient up till now. As the main results of this study, the data on the polarity and magnitude of the primary electrostatic charges of ballistic basidiospores were measured, registered, and analyzed. Secondly, the magnitude of the hymenial emission rate of charged spores was measured and analyzed. The upper limit for the emission rate was estimated. Third, the equation for the charge relaxation time of spores was derived, and corresponding relaxation time was estimated.

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