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# Bioaerosols on the atmospheric super highway: An example of long distance transport of *Alternaria* spores from the Pannonian Plain to Poland

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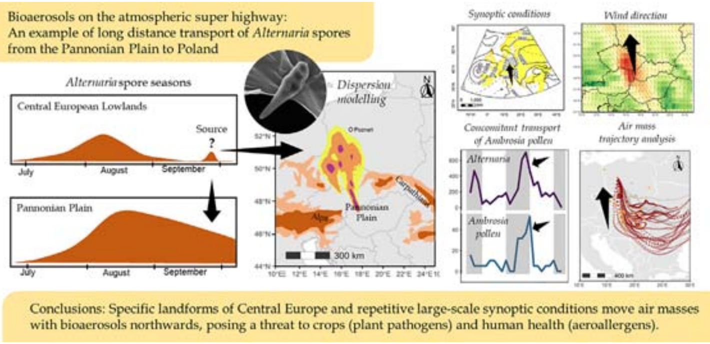
## HIGHLIGHTS

- Airborne *Alternaria* spores are transported from South to Central Europe.
- The source of spores is located in northwest part of Pannonian Plain.
- Long-distance transported (LDT) spores are deposited at night or early morning.
- LDT is confirmed by the presence of non-local ragweed pollen.
- LDT *Alternaria* spores may pose a risk to both human and plant health.

## GRAPHICAL ABSTRACT



Bioaerosols on the atmospheric super highway:
An example of long distance transport of *Alternaria* spores from the Pannonian Plain to Poland

Conclusions: Specific landforms of Central Europe and repetitive large-scale synoptic conditions move air masses with bioaerosols northwards, posing a threat to crops (plant pathogens) and human health (aeroallergens).

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## ABSTRACT

*Alternaria* spores are pathogenic to agricultural crops, and the longest and the most severe sporulation seasons are predominantly recorded in rural areas, e.g. the Pannonian Plain (PP) in South-Central Europe. In Poland (Central Europe), airborne *Alternaria* spore concentrations peak between July and August. In this study, we test the hypothesis that the PP is the source of *Alternaria* spores recorded in Poland after the main sporulation season (September–October).
Airborne *Alternaria* spores (2005–2019) were collected using volumetric Hirst spore traps located in 38 locations along the potential pathways of air masses, i.e. from Serbia, Romania and Hungary, through the Czech Republic, Slovakia and Ukraine, to Northern Poland. Three potential episodes of Long Distance Transport (LDT) were selected and characterized in detail, including the analysis of *Alternaria* spore data, back trajectory analysis, dispersal modelling, and description of local weather and mesoscale synoptic conditions.
During selected episodes, increases in *Alternaria* spore concentrations in Poznań were recorded at unusual times that deviated from the typical diurnal pattern, i.e. at night or during morning hours. *Alternaria* spore concentrations on the PP were very high (>1000 spores/m$^3$) at that time. The presence of non-local *Ambrosia* pollen, common to the PP, were also observed in the air. Air mass trajectory analysis and dispersal modelling showed that the northwest part of the PP, north of the Transdanubian Mountains, was the potential source area of *Alternaria* spores.
Our results show that *Alternaria* spores are transported over long distances from the PP to Poland. These spores may markedly increase local exposure to *Alternaria* spores in the receptor area and pose a risk to both human and plant health. *Alternaria* spores followed the same atmospheric route as previously described LDT ragweed pollen, revealing the existence of an atmospheric super highway that transports bioaerosols from the south to the north of Europe.

## 1. Introduction

Plant pathogens cause a substantial loss in the quality and quantity of crop yield, reducing food security at national and global levels (Savary et al., 2019). Some of the most economically devastating pathogens belong to plant pathogenic fungi (Dean et al., 2012; Doehlemann et al., 2017). Fungi have developed a broad repertoire of effective strategies to facilitate host colonization, like intensive spore production, formation of appressorium, release of cell wall degrading enzymes, or suppression of plant defence reactions (Lo Presti et al., 2015). Consequently, fungal pathogens cause severe damage to a large number of economically important fruits, vegetables, and crops at both pre- and post-harvest stages (Dean et al., 2012).

The genus *Alternaria* comprises a group of fungi in the family Pleosporaceae (Pleosporales, Dothideomycetes, Ascomycota) (Lawrence et al., 2016) that includes both saprotrophic and endophytic species as well as necrotrophic pathogens with a broad host range (Barnes, 1979). Collectively, *Alternaria* spp. cause a range of diseases on numerous species of agronomic importance, including cereals, ornamentals, oil crops, vegetables, and fruits (Thomma, 2003). Some of the most important plant damaging species include *Alternaria brassicae*, *A. brassicicola*, *A. alternata*, *A. raphani*, *A. solani*, *A. dauci*, and *A. tenuissima* (Barnes, 1979; Rajarammohan et al., 2019). *Alternaria brassicae* and *A. brassiciola* are the main causal agents of black spot disease in a large variety of host plants in the Brassicaceae family, e.g. oilseed rape, cabbage, radish, cauliflower, resulting in 20 to 50% yield reductions in crops (Barnes, 1979; Cho, 2015). *Alternaria alternata* is known as the cause of brown leaf spot, rots, blights, and other diseases in over 100 host species of plants (e.g., tomato, chili, potato, and citrus) as well as postharvest diseases in various crops (Meena and Samal, 2019; Woudenberg et al., 2015).

Since *Alternaria* spp. are pathogenic to agricultural crops, the highest concentrations of airborne *Alternaria* spores are predominantly recorded in rural areas, especially with high amounts of cereals and oilseed rape (Apangu et al., 2020; Kasprzyk et al., 2015; Skjøth et al., 2016). Within a certain biogeographical region, a positive correlation between the abundance of agricultural land and amount of *Alternaria* spores has been observed in Europe (Grinn-Gofroń et al., 2020; Skjøth et al., 2016). Similarly, in the United States, the distribution of *A. alternata* in dust samples coincided with the Great Plains area, i.e. a region of extensive cattle ranching and farming (Dietzel et al., 2019). In addition, the seasonal peak in the concentration of *Alternaria* spores has been shown to be related to specific agricultural operations, like crop harvesting, that can release extremely high levels of spores into the air (between $1.2 \times 10^{10}$ and $6.7 \times 10^{10}$ *Alternaria* spores ha$^{-1}$) (Apangu et al., 2020; Skjøth et al., 2012; Van der Waals et al., 2003). Daily increases in the concentration of airborne *Alternaria* spores during the season is also greatly impacted by local meteorological conditions, especially high daily mean temperature and low relative humidity (Aira et al., 2013; Grewling et al., 2020; Jambhulkar et al., 2016). *Alternaria* spores are produced on elongated conidiophores and are passively dispersed in warm, dry weather by physical disturbances, e.g. turbulences of wind and natural shaking of leaves (Van der Waals et al., 2003). Furthermore, in dry air, conidiophores may undergo twisting movements with varying degrees of violence, dissecting and scattering spores in all directions (Meredith, 1973).

The release mechanisms of spores impacts both their temporal and spatial distribution in the air. *Alternaria* spores are present in the greatest concentrations on dry, warm, and windy afternoons (Olsen et al., 2020; Skjøth et al., 2012; Stępalska and Wołek, 2009) and, within a certain environment (e.g., wheat fields), are more abundant in dryer and warmer places (Schiro et al., 2018). As the sporulation season of *Alternaria* is mainly limited to warm dry weather and adapted to the growing season of the host plants, therefore a distinct geographical pattern in certain characteristics of the *Alternaria* spore season is observed in Europe. For instance, the start and length of the season and the day with maximum spore concentration show a gradient from south to north having a positive correlation with latitude (Kasprzyk et al., 2015; Skjøth et al., 2016). The sporulation season of *Alternaria* is up to 4 months longer in southern Europe than in the north, e.g. ranging from 2 to 3 months in Denmark to 6–7 months in Greece (Skjøth et al., 2016). In Poland, the main peak in *Alternaria* spore concentrations in the air occurs between July and August, and the level of spores decrease markedly in September (Grewling et al., 2019b; Kasprzyk et al., 2013a). However, sudden increases in the *Alternaria* spore levels were also recorded after the main sporulation season (Grewling et al., 2019b; Kasprzyk et al., 2013b). It has recently been revealed that elevated levels of *Alternaria* spores were observed in the air during the long-distance transport of ragweed pollen (*Ambrosia* sp.) from the Pannonian Plain to Poland (Grewling et al., 2019a). It has been suggested that *Alternaria* spores could be released in agricultural areas of the Pannonian Plain and transported north,similar to the mechanism described for ragweed pollen (Šikoparija et al., 2013).

In this study, we test the hypothesis that the Pannonian Plain is the source of post-seasonal *Alternaria* spores recorded in the Central European Lowlands. The following objectives were used to achieve this goal: (1) The collection and statistical analysis of airborne *Alternaria* spore data from 38 monitoring stations in Central Europe (located along the potential pathways of air masses, i.e., from Hungary, through Slovakia and Czech Republic, to northern Poland); (2) The subsequent selection of potential LDT episodes; (3) The investigation of air mass back-trajectory analyses during LDT episodes; (4) The modelling of particle dispersion from the source area; (5) In-depth characterization of synoptic and climatic conditions recorded during air mass movements.

## 2. Materials and methods

### 2.1. *Alternaria* spore data collection

The monitoring of airborne *Alternaria* spores was conducted over 15 years (2005–2019) in 38 locations in Europe (Fig. 1, Table S1). *Alternaria* spores were collected by 7-day volumetric traps (Hirst, 1952) located at roof level. Air containing fungal spores was sucked into the trap (10 l/min) and impacted on the adhesive tape that was later divided into segments corresponding to 24 h periods. Each segment was mounted on a microscope slide and spores were morphologically examined by light microscopy. Spores of different *Alternaria* species are very similar (Simmons, 2007). As a result, *Alternaria* spores are identified to genus level during routine aerobiological monitoring based on spore morphology. Spores were counted following the standard methods described by Mandrioli et al. (1998) (Table S1). Daily average (00:00–24:00) *Alternaria* spore counts were converted into concentrations and expressed as spores/m$^3$ (Galán et al., 2017).

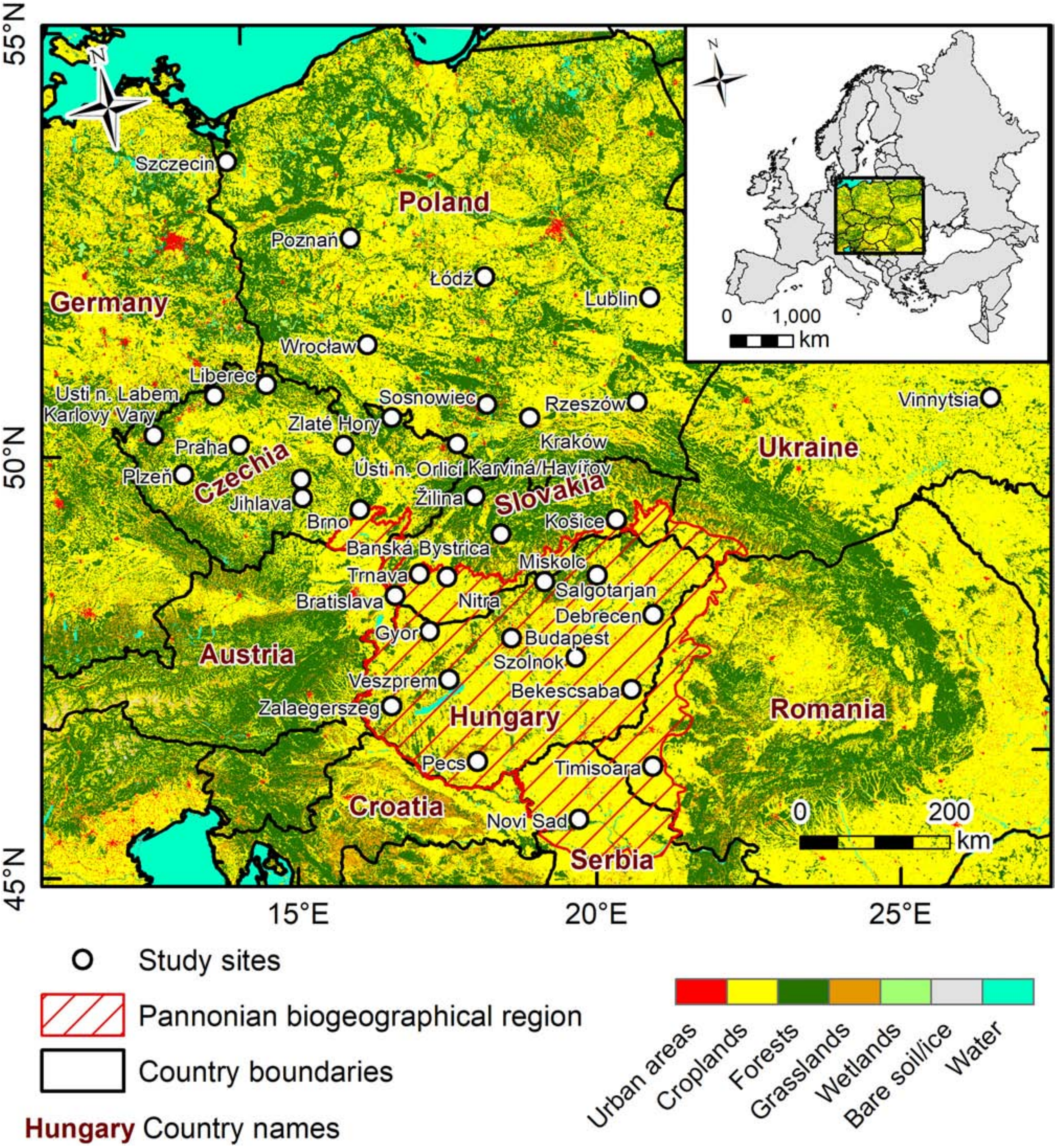

**Fig. 1.** Study area with selected fungal spore monitoring stations.

### 2.2. Analysis of Alternaria spore data

The *Alternaria* spore database from Poznań (Western Poland) was screened to select potential episodes of long-distance transport (LDT). Potential LDT episodes were selected based on the following criteria: (1) The daily average *Alternaria* spore concentration recorded in Poznań exceeded 100 spore/$m^3$, i.e. the clinical threshold level that is believed to evoke the first allergy symptoms (Gravesen, 1979); (2) The peak *Alternaria* spore concentration was recorded during night hours, deviating from the typical diurnal pattern observed in the city (Fig. S1) and, therefore, indicating the influx of non-local *Alternaria* spores as it often observed in the case of pollen grains transported from remote sources (Šikoparija et al., 2013; Smith et al., 2008; de Weger et al., 2016); (3) Episodes were recorded after 15th September, i.e. after the main sporulation season (Grewling et al., 2019b; Kasprzyk et al., 2013a); (4) Air masses arrived in Poznań from a southerly direction; (5) High concentrations of *Alternaria* spores (>1000 spores/$m^3$) were also observed on the Pannonian Plain during these episodes.

### 2.3. Air mass back trajectory and atmospheric dispersion modelling

Backward air mass trajectories were calculated using the Hybrid Single Particle Lagrangian Integrated Trajectory model (HYSPLIT) (Rolph et al., 2017; Stein et al., 2015). This approach has been previously employed for numerous airborne fungal spore studies in order to detect potential source area of spores (Fernandez-Rodriguez et al., 2015; Grinn-Gofroń et al., 2016; Sadyś et al., 2014; Skjøth et al., 2012). Global Data Assimilation System (GDAS) meteorological data with a spatial resolution of 0.5° × 0.5° were applied. HYSPLIT trajectories were calculated 72 h back in time with 2 h steps between each trajectory (thus 12 trajectories each day), which corresponds to the time step of the bihourly *Alternaria* spore observations. Trajectories associated with two different bi-hourly *Alternaria* spore concentration levels, i.e. indicated as low (0–200 spore/$m^3$) and high level (>200 spore/$m^3$) has been additionally selected. Three starting heights of back-trajectories: 500 m, 1000 m, and 1500 m have been chosen, to take into account variations in air mass directions with increasing altitude.

Back trajectory analysis only shows the pathways of air masses, and multiple areas can be associated with the potential sources at different times (Williams and Barneoud, 2021). Therefore, in order to identify the exact source area from which the *Alternaria* spores were released, monitoring stations located along the path of the trajectories with the highest bi-hourly atmospheric *Alternaria* spore concentrations that coincided with the passage of the air masses were selected for further analysis. The movement of *Alternaria* spores emitted from the area of these stations during selected LDT episodes was simulated using the HYSPLIT dispersion model (Rolph et al., 2017; Stein et al., 2015).

We calculated the forward HYSPLIT dispersion of particles with a settling velocity of 0.047 cm/s, which is the mean value estimated for *Alternaria* spores (Gregory, 1973; Woo et al., 2018). To ensure compatibility with the back-trajectory analysis, the simulations were performed using GDAS 0.5° × 0.5° resolution meteorological data. The particle release starting time was set according to the back-trajectory time (separately for each specific episode), while the release duration was set to 6 h. The release top and bottom heights were set to 1 m and 0 m, respectively, to indicate the release of spores from low vegetation, plant debris and the soil surface. Runtime parameters, i.e. the total duration of the simulation, were set to 48 h, with an averaging period of 2 h and a top of averaged layer of 100 m a.g.l. (to represent the layer where the spores could have been initially emitted), similarly as in Apangu et al. (2020). As the exact release quantity of spores was unknown, we set this parameter as 1 unit of mass (as recommended by HYSPLIT developers). Therefore, the resulting concentrations represent a dilution factor (1/$m^3$) instead of true air concentrations and provide a “footprint” of the dispersion pattern. The HYSPLIT model setup covers simulations for both dry and wet particle deposition that takes into account both in cloud and below cloud scavenging.

### 2.4. Atmospheric circulation pattern and weather data

The atmospheric circulation patterns during the selected LDT episodes were classified using the ‘environment to circulation’ approach, i.e., a specific set of environmental criteria for a particular phenomenon (Dayan et al., 2012; Yarnal, 1993). Thus, to reveal the large-scale pressure patterns that control the possibility of the influx of *Alternaria* spores to Poland, we analysed the mean sea level pressure (SLP) and 500 hPa geopotential height (z500), which were expressed in hPa and m a.s.l., respectively. The data were extracted from the NCEP/NCAR reanalysis data (Kalnay et al., 1996). The spatial resolution of all NCEP/NCAR reanalysis data used here was 2.5° × 2.5°, extending from 35° to 70°N and from 20°W to 40°E (as in Bogawski and Bednorz (2016)). The composite maps of SLP and z500 were constructed for every LDT episode. Next, these maps were related to the long-term (2010–2019) mean values of the SLP and z500 in the September–October period (shown in the Supplementary Materials), i.e. the period when all the selected LDT episodes occurred. Finally, anomaly maps were produced showing differences between the pressure patterns of LDT episodes and the long-term mean.

Local daily weather station data, i.e. rainfall (mm), mean temperature (°C), humidity (%) and local wind speed (m/s) and direction (°) were obtained from the OGIMET database (http://ogimet.com/index.phtml.en) extracted with R package ‘climate’ (Czernecki et al., 2020). Local wind data were visualized using the R package ‘openair’ (Carslaw and Ropkins, 2012). To continuously represent wind field, the three-hour surface wind speed (m/s) and wind direction data were also downloaded from the NOAA Global Forecasting System website (https://www.ncdc.noaa.gov/data-access/model-data/model-datasets/global-forcast-system-gfs) and analysed using the ‘rWind’ package (Fernandez-Lopez and Schliep, 2019).

## 3. Results

During the studied period (2005–2019), we have identified 121 days with *Alternaria* spore concentrations over 100 spores/$m^3$, that occurred after 15th of September. The analysis of air mass back-trajectories revealed that during 55% of days (67 in total) air masses arrived from south or south-easterly directions, indicating the region of the Pannonian Plain as a possible source of *Alternaria* spores. In total, 14 potential LDT episodes of *Alternaria* spores were identified. These episodes showed a similar pattern with respect to the direction of the influx of air masses, the duration of the episodes, and the location of the spore source. For brevity, ultimately, only three post-seasonal episodes with elevated *Alternaria* spore concentrations were chosen and investigated in detail: 24–25 September 2010 (Episode I), 18–19 September 2014 (Episode II), and 3–4 October 2015 (Episode III) (Fig. S2).

### 3.1. Episode I (24–25 September 2010)

Daily average concentrations of airborne *Alternaria* spores increased from 16 spores/$m^3$ on 22 September 2010 to 280 spores/$m^3$ on 25 September (Fig. S2). The highest bi-hourly *Alternaria* spore concentration recorded in Poznań was 747 spores/$m^3$ at 03:00 (on 24 September) (Fig. 2). The presence of *Ambrosia* pollen was also observed in the air between 22 and 25 September. Atmospheric concentrations of *Alternaria* spores and *Ambrosia* pollen concomitantly increased during night-time hours. Back-trajectory analysis showed that, before arriving in Poznań, the air masses passed mainly over the Czech Republic, Slovakia, Austria and Hungary (Fig. 3). Three monitoring stations in Hungary (i.e. Budapest, Győr and Veszprém) recorded mean daily average *Alternaria* spore concentrations in excess of 1000 spores/$m^3$ on 23 September, and Veszprém recorded 3648 *Alternaria* spores/$m^3$ (daily average) on 24 September 2010. High daily average *Alternaria* spore concentrations were also recorded in Czech Republic and Slovakia (798 spores/$m^3$ in Zlaté Hory, and 624 spores/$m^3$ in Trnava, respectively). At monitoring stations located further south and east, e.g., Timisoara (Romania) and Vinnytsia (Ukraine), the concentrations of *Alternaria* spores were much lower (<250 spores/$m^3$). Low daily *Alternaria*

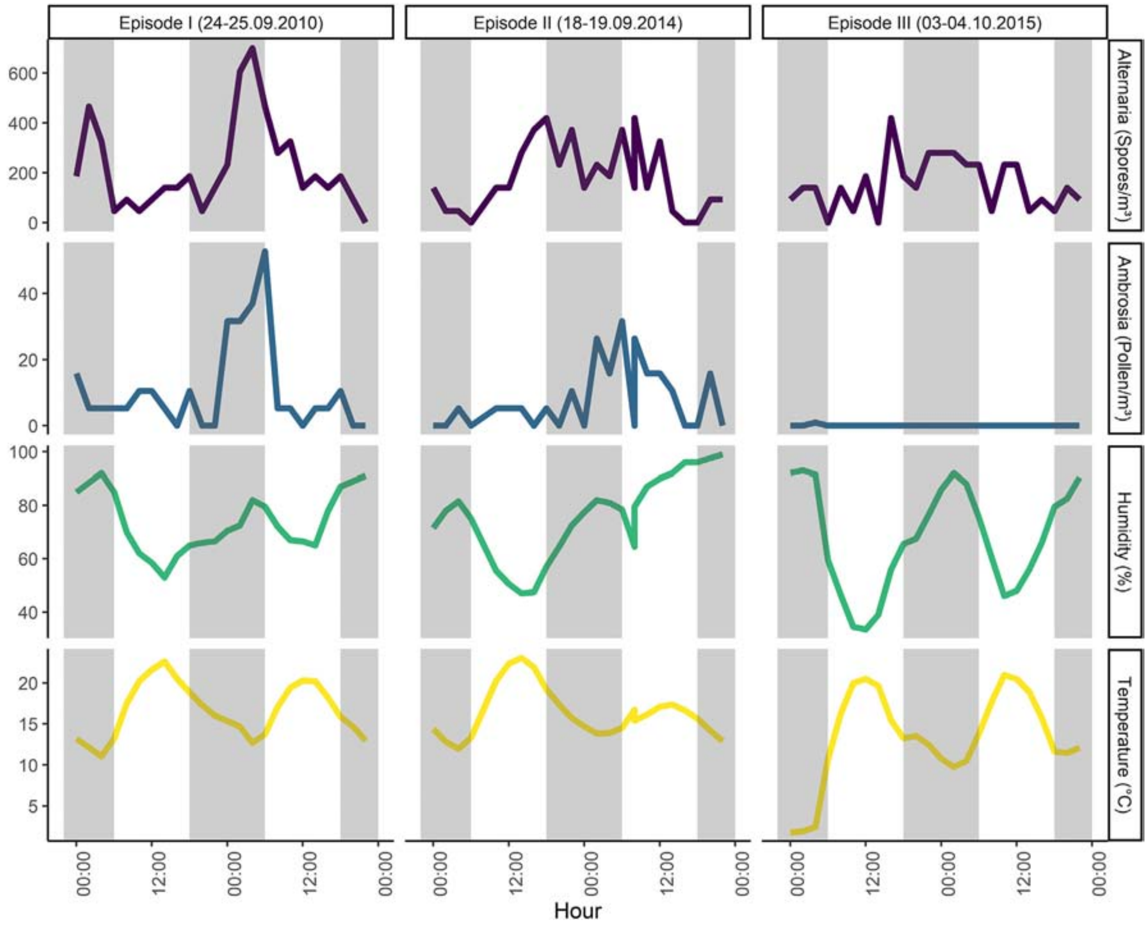

**Fig. 2.** Diurnal variation in daily mean temperature, humidity, *Alternaria* spore and *Ambrosia* pollen concentrations during investigated episodes (night-time hours are indicated in grey).

spore concentration (max. 75 spores/m$^3$) was also recorded in Szczecin (Northern Poland) (Table S2).

Dispersion analysis showed that particles released from the Pannonian Plain between 12:00–18:00 on 24 September 2010 would arrive in Western Poland within ~12 h and be deposited after midnight (Fig. 4). In the following hours the spores could be transported over northern Poland. During the period 24–25 September 2010 the synoptic situation was dominated by a high pressure centre in the east in the vicinity of European Russia and a

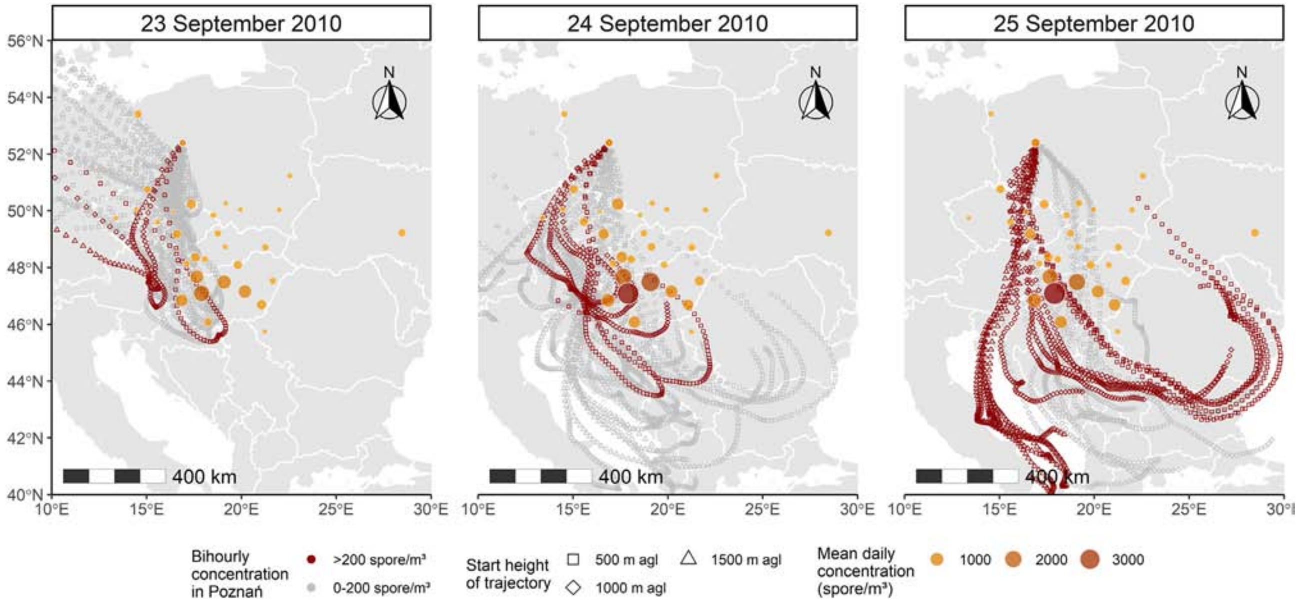

**Fig. 3.** Back trajectory analysis showing the path taken by air masses arriving in Poznań, 23–25 September 2010.

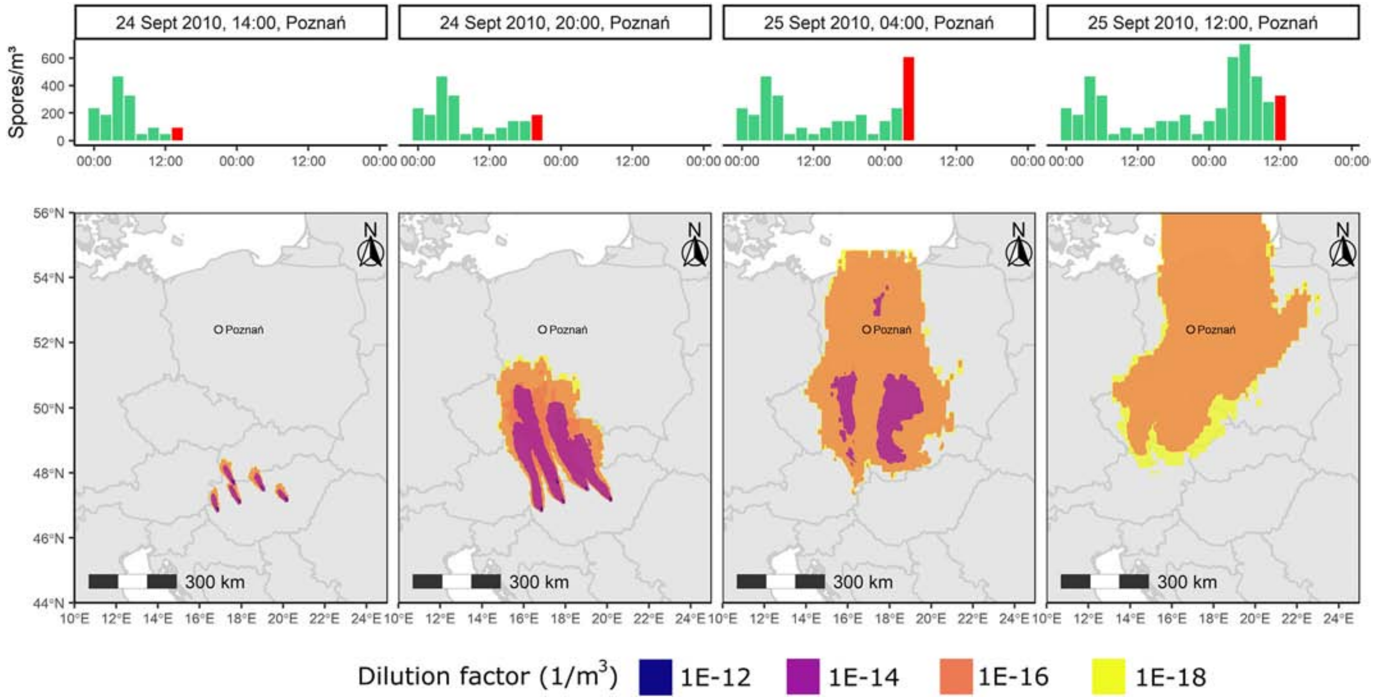

**Fig. 4.** Top panel: Bi-hourly *Alternaria* spore concentration recorded in Poznań between 24 and 25 September 2010 (the red bars indicate the time corresponding to the dispersion analysis). Bottom panel: Dispersion of air particles released over potential source areas calculated using HYSPLIT (starting time – 12:00, 24 September 2010, see Methods section for model parameters).

low pressure centre in the west over the Atlantic, facilitating the stable northerly movement of air masses (Figs. 5, S3, S4). Winds measured at stations on the Pannonian Plain were from the Southeast, reaching a maximum of 6–7 m/s (Fig. S5). No significant rainfall was recorded in the source areas or along the path travelled by air masses during the period 22–25 of September. In contrast, heavy rainfall was recorded in the source area on 26 September (Fig. S6). Although no rain was recorded that day in Western Poland, daily average concentrations of *Alternaria* spores dropped dramatically to 8 spores/m$^3$ (Fig. S2).

### 3.2. Episode II (18–19 September 2014)

An increase in atmospheric concentrations of *Alternaria* spores was recorded in Poznań during 18–19 September 2014, and was characterized by two distinct peaks. The first peak was between 16:00 and 20:00 on the 18 September and the second between 06:00 and 10:00 on the 19 September (Figs. 2, S2). During the second peak, elevated concentrations of airborne *Ambrosia* pollen were also observed (daily average concentration reached 30 pollen/m$^3$). Back trajectory analyses show that air masses arriving at Poznań on the 18 and 19 September came from a southerly direction passing over the Balkans, Hungary, Austria, Slovakia, and Czech Republic (Fig. 6).

During the period 16–18 September 2014 very high daily average concentrations of airborne *Alternaria* spores were recorded at monitoring sites in Hungary (i.e. >1000 spore/m$^3$ at Debrecen, Győr, Szolnok, Veszprém, Miskolc, and Békéscsaba) and the Czech Republic (i.e. >6000 spore/m$^3$ in Zlaté Hory on 18 September). Much lower *Alternaria* spore concentrations (<250 spore/m$^3$) were recorded in Serbia, Ukraine and southern Poland (Table S2). At this time, winds on the Pannonian Plain were from the southeast, and wind speeds reached their maximum at midday (~10 m/s) (Fig. 7, Fig. S7).

Modelled dispersion of *Alternaria* spores released over the Pannonian Plain at midday on 18 September 2014 show that the plume travelled in a North-easterly direction, reaching Poznań in the early morning of 19 September before moving to northern Poland and Germany (Fig. 8). On September 18 and 19, only sporadic rainfall was observed along the transport route of the spores (Fig. S6). Synoptic conditions were very similar to those witnessed during Episode I (Fig. 5), but with a larger pressure gradient which explains the higher wind speeds in the source area (Figs. S8, S9).

### 3.3. Episode III (3–4 October 2015)

Daily average *Alternaria* spore concentrations recorded in Poznań during 1–4 October 2015 exceeded 100 spores/m$^3$, with a peak of 163 *Alternaria* spores/m$^3$ daily average on 4 October (Fig. S2). Bi-hourly *Alternaria* spore concentrations increased to 420 spores/m$^3$ at 16:00–18:00 on the 3 October. Elevated *Alternaria* spore concentrations persisted till 14:00 the next day. Between 02:00–06:00 on 4 October, bi-hourly *Alternaria* spore concentrations exceeded 200 spores/m$^3$ (Fig. 2). During the period 1–4 October 2015, the air masses approaching Poznań gradually veered from the Northeast to the Southwest. Air masses arriving in Poznań at the time of highest *Alternaria* spore concentrations had traversed the western part of the Carpathian Mountains and the Sudetes. Back trajectory analysis shows that possible sources of *Alternaria* spores on 3–4 October 2015 included the Czech Republic, central Austria, western Slovakia and Hungary (Fig. 9). On 3 October, the monitoring station at Trnava (western Slovakia) recorded 1023 *Alternaria* spores/m$^3$ (daily average concentrations) (Table S2). High daily average *Alternaria* spore concentrations were observed over Hungary, e.g. in Győr and Szolnok (1728 and 1248 spores/m$^3$, respectively). The highest *Alternaria* spore levels in the Czech Republic was 435 spores/m$^3$ recorded in Jihlava. In Novi Sad (Serbia) the daily average *Alternaria* spore concentration reached 304 spores/m$^3$. A similarly high concentration of *Alternaria* spores was also recorded in Rzeszów (south-eastern Poland). The direction and strength of the wind on 03 October 2015 were similar to those observed during Episode II in 2014 (Fig. S10). A distinct belt of strong winds stretched from northern Hungary, through Slovakia and the Czech Republic, to southern Poland (Fig. 10).

Dispersion analysis showed that *Alternaria* spores released over the Pannonian Plain at midday on 3 October 2015 were directed to the north, reaching Poznań in the early morning of 4 October, and then transported to the Northeast (all the way to Lithuania and the Kaliningrad Oblast)

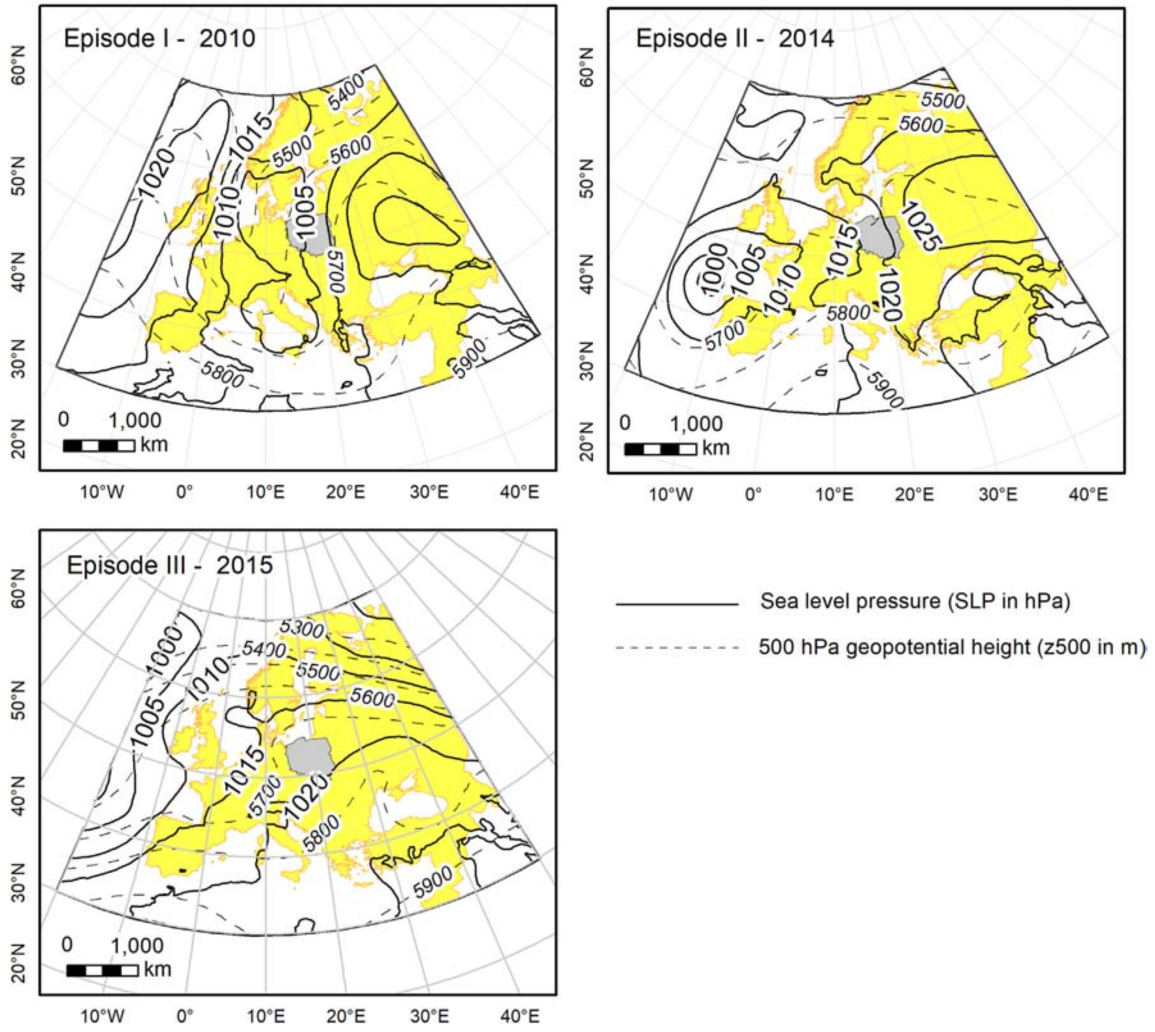

**Fig. 5.** Sea level pressure (solid contours) and 500 hPa geopotential height (dashed contours) during the episodes.

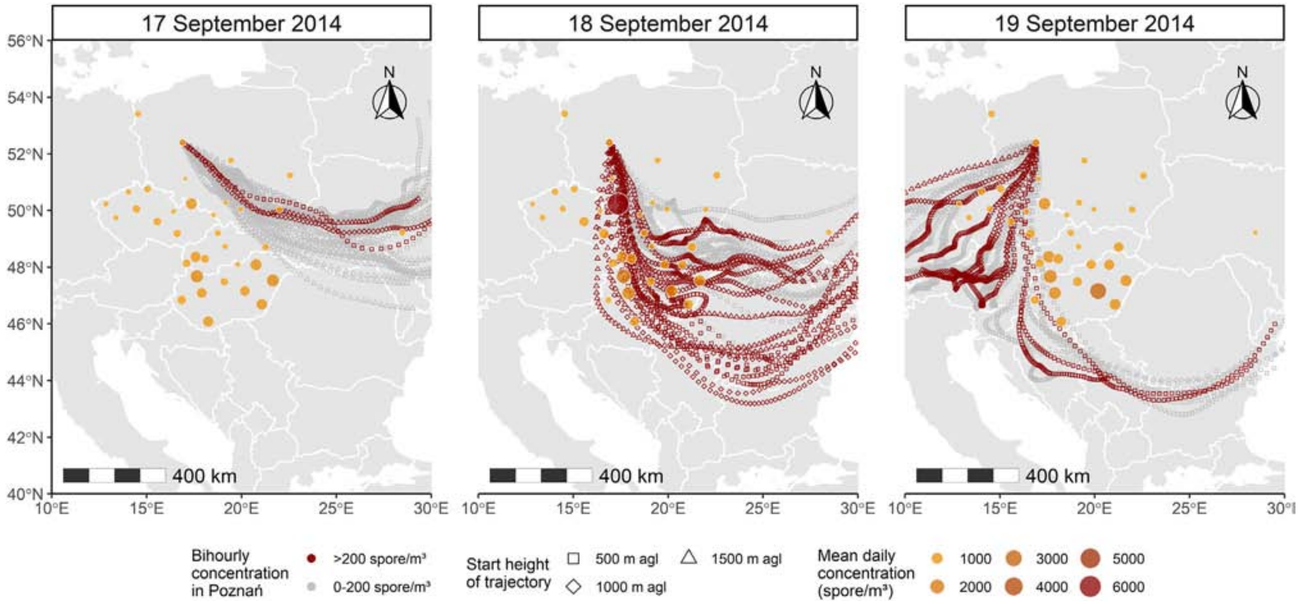

**Fig. 6.** Back trajectory analysis showing the path taken by air masses arriving in Poznań, 17–19 September 2014.

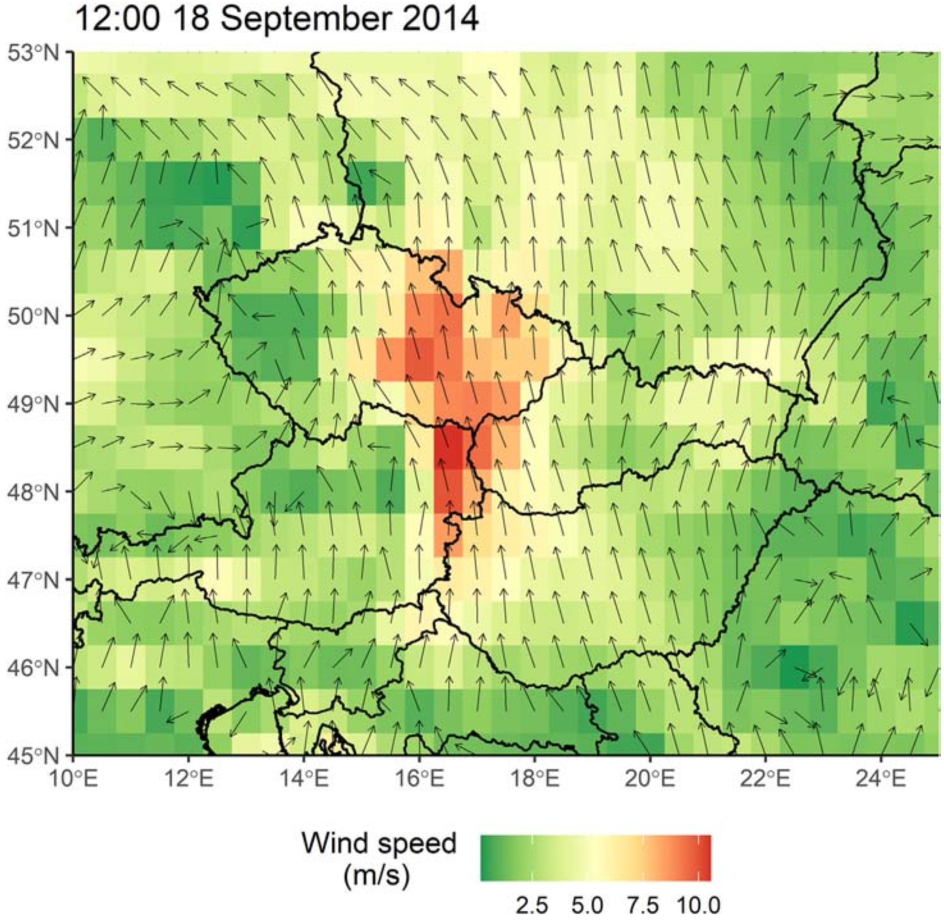

**Fig. 7.** Wind speed and direction over source area at 12:00 18 September 2014.

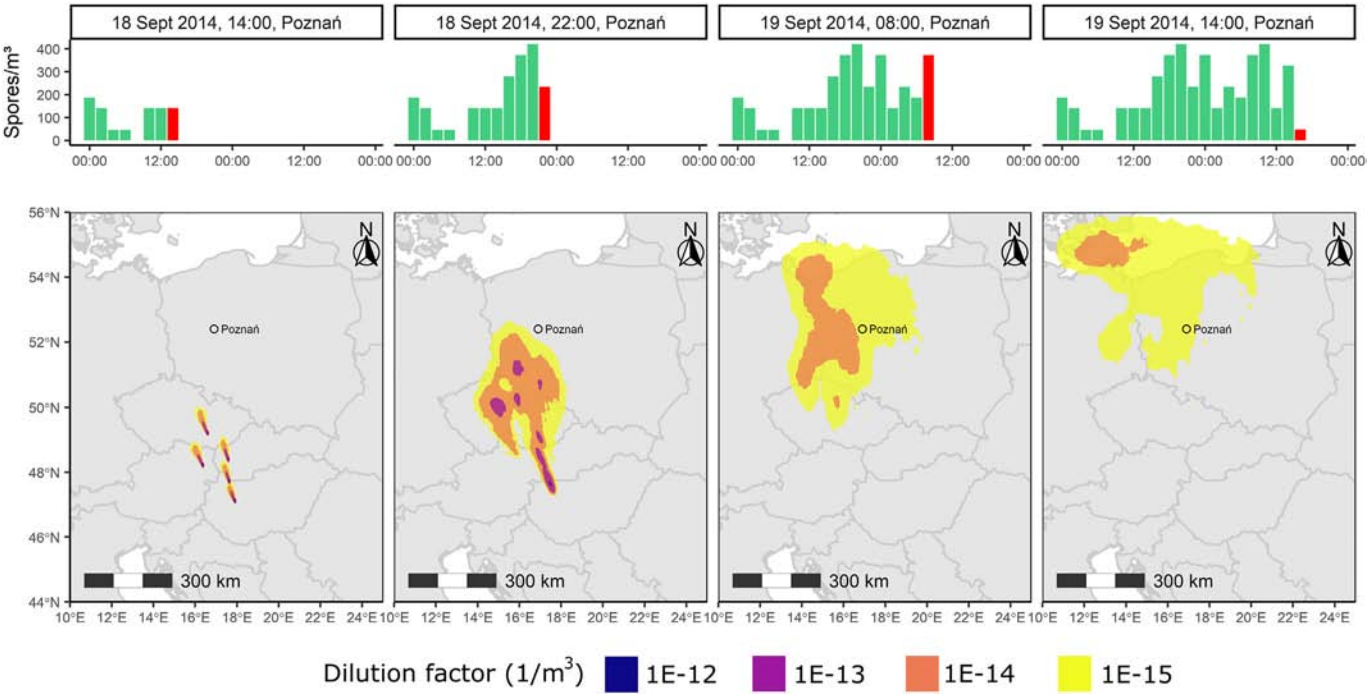

**Fig. 8.** Top panel: Bi-hourly *Alternaria* spore concentration recorded in Poznań between 18 and 19 September 2014 (the red bars indicate the time corresponding to the dispersion analysis). Bottom panel: Dispersion of air particles released over potential source area based on HYSPLIT model (starting time – 12:00, 18 September 2014).

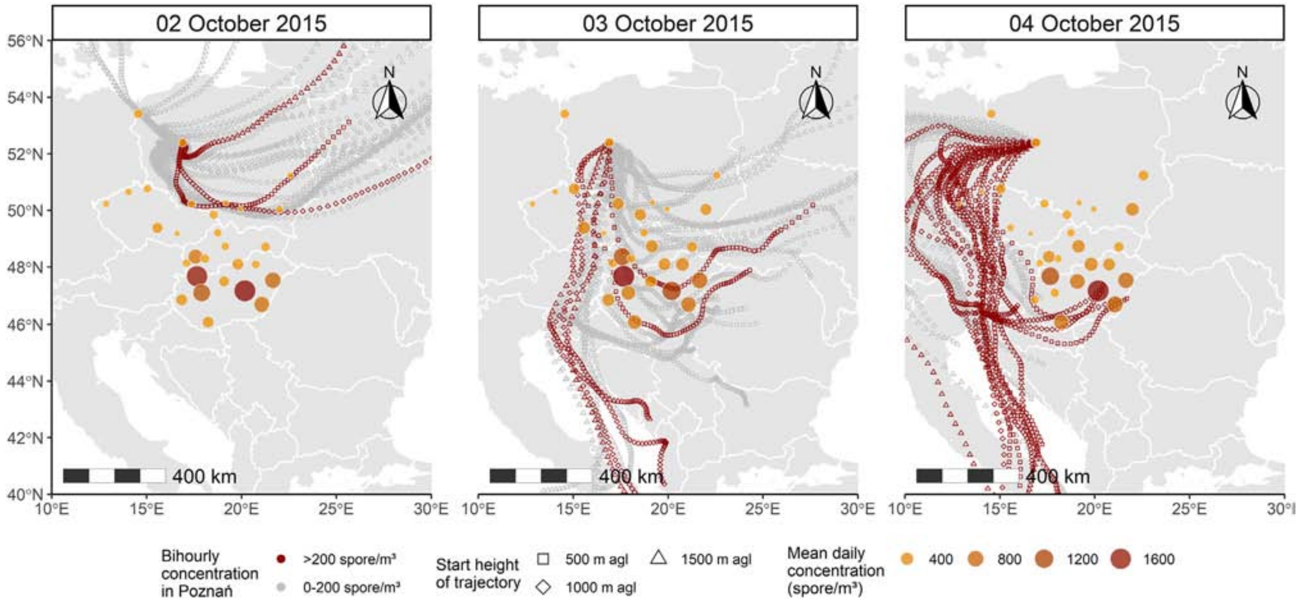

**Fig. 9.** Back trajectory analysis showing the path taken by air masses arriving in Poznań, 02–04 October September 2015.

(Fig. 11). There was practically no rainfall in the source area during these days (Fig. S6). On 5 October, heavy rainfall was however observed on the Pannonian Plain. On that day, a decrease in the concentration of *Alternaria* spores (daily average concentration reached only 47 spores/m$^3$) was recorded in Poznań. The synoptic situation was more dynamic than during previous episodes and changed from hour to hour (Figs. S11, S12), although it was generally characterized by Low pressure to the North and West and High pressure to the South and East. In more detail, a high pressure centre was first located over the source area, the descending air meant that no transport was possible. Starting from 3 October, the High

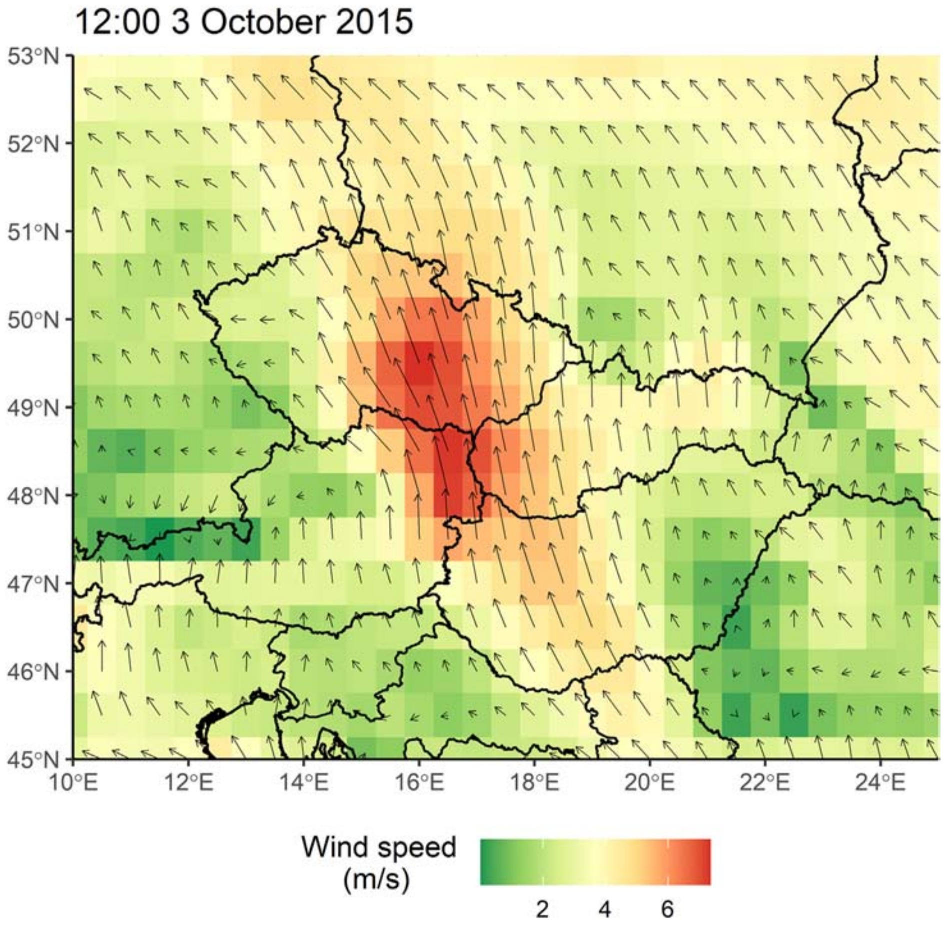

**Fig. 10.** Wind speed and direction over source area at 12:00 03 October 2015.

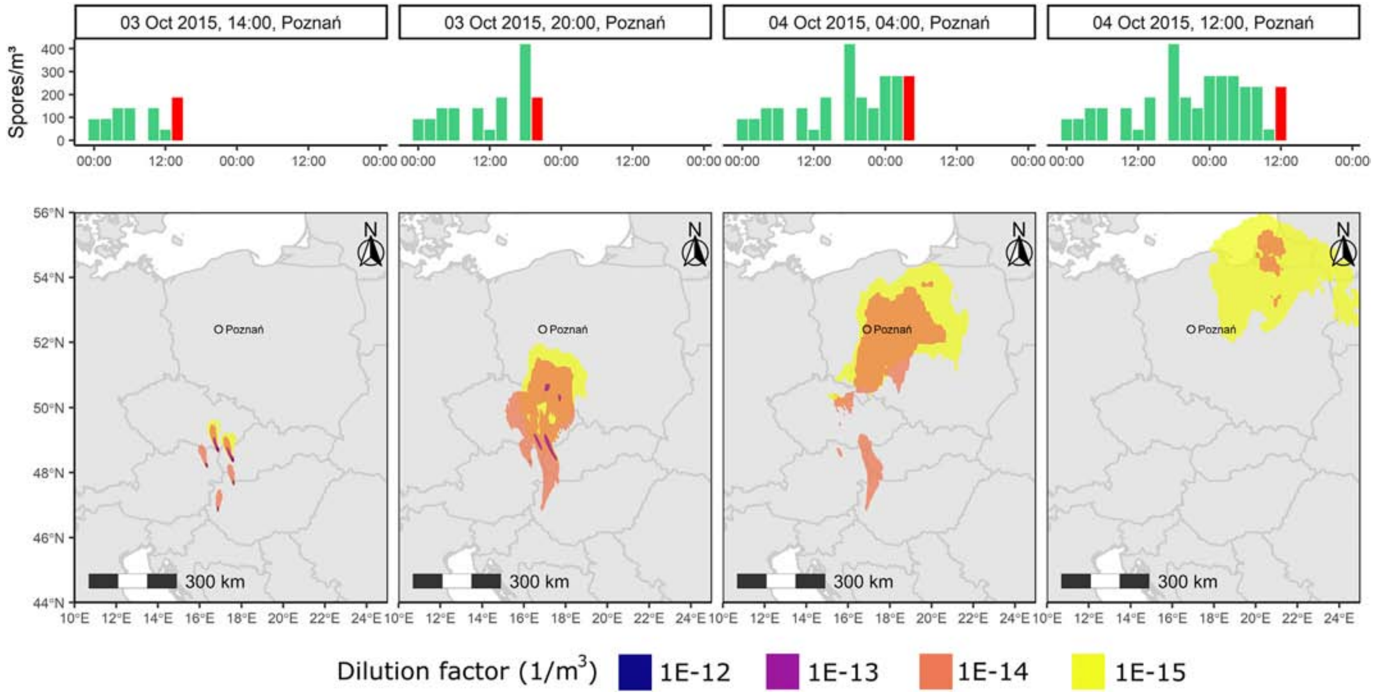

**Fig. 11.** Top panel: Bi-hourly *Alternaria* spore concentration recorded in Poznań between 3 and 4 October 2015 (the red bars indicate the time corresponding to the dispersion analysis). Bottom panel: Dispersion of air particles released over potential source area based on HYSPLIT (starting time – 12:00, 3 October 2015).

pressure moved to the East facilitating air movement to the North and East (Fig. 5).

## 4. Discussion

### 4.1. The source region of Alternaria spores

The analysis of *Alternaria* spore data, back trajectories, dispersal modelling, and description of local weather and mesoscale synoptic conditions conducted in this study supports the hypothesis that LDT *Alternaria* spores recorded in Poznań mainly originate in the Great Pannonian Plain. More specifically, the source area can be limited to the north-western part of the Plain, including the Danubian Lowland in western Slovakia (with cities Trnava, Bratislava and Nitra), the Little Hungarian Plain in south-western Hungary (Győr, Zalaegerszeg and Veszprém), and the South Moravian lowlands in eastern Czech Republic (Brno) (Fig. 1). This area is divided from the main Great Pannonian Plain by the Transdanubian (Bakony) Mountains (up to 750 m a.s.l.) that run southwest-northeast for over 100 km from the Zala River and may serve as an orographic barrier to air masses travelling from the Great Pannonian Plain in the southeast. During investigated LDT episodes, the daily average concentrations of *Alternaria* spores recorded at monitoring stations located in the source area, e.g. in Győr, Budapest, Veszprém, Zalaegerszeg, Trnava and Brno, were very high often reaching hundreds of spores per cubic metre of air. After release from the source area, *Alternaria* spores travelled north and passed through the Sudeten range (~ 1500 m a.g.l.) between the Czech Republic and Poland. It is likely that air masses moved over the Sudetes through natural depressions, e.g. the Lusatian Gate in the west (240 m a.g.l), the Kłodzko Valley in the centre (400 m a.g.l), and the Moravian Gate in the east (300 m a.g.l.). It has already been documented that the Moravian Gate serves as a natural opening through which air masses passing from south to north can transport bioaerosols to Poland (Grewling et al., 2016; Šikoparija et al., 2013). Overall, *Alternaria* spores travelled more than 600 km from the source area in the north-western part of the Great Pannonian Plain to Western Poland.

Several hundred kilometres seems like a long distance, especially considering the large size of *Alternaria* spores. It was suggested that the air dispersal of *Alternaria* spores is predominantly local (even at the field level), and the role of local sources as having the greatest influence on *Alternaria* spore concentration was previously highlighted (Grinn-Gofroń et al., 2020; Olsen et al., 2019). It has, however, been reported that under certain synoptic conditions, a significant amount of *Alternaria* spores could be transported over much greater distances (Skjøth et al., 2012). Experiments in Copenhagen (Denmark) showed that high concentrations of *Alternaria* spores were associated with air masses arriving from agricultural areas in northern Germany and Poland (located over 300 km from Copenhagen) (Skjøth et al., 2012). A similar phenomenon was also observed in Great Britain (Sadyś et al., 2015) and Spain (Fernandez-Rodriguez et al., 2015). *Alternaria* spores have also been isolated from air samples taken from a height of several kilometres above ground (Browne, 1930; Damialis et al., 2017; Hirst et al., 1967; Stakman et al., 1923). Many examples of the presence of *Alternaria* spores in the air over isolated and unfavourable areas, e.g. the Arctic, have been cited by Gregory (1973). All these studies show that *Alternaria* spores, despite the large sizes, can be transported for long distances, even hundreds of kilometres.

The entire distance, from the source region to western Poland, was covered by *Alternaria* spores in 16–22 h. Spores were released around noon, when the increase in wind speed (>2.0 m/s) was observed over the Pannonian Plain. Midday corresponds to the highest release rate of *Alternaria* spores estimated on the basis of field observations (Gregory, 1973). Furthermore, previous studies (Rotem, 1991; Rotem, 1994) showed that *Alternaria* spores are already detached at moderate wind speeds (0.4 and 1.0 m/s). However, even in almost windless conditions, the spores can be released into the air if there are occasional gusts of wind. *Alternaria* spores reached Poland in the early morning of the following day (4:00–10:00) after a full day of travel.

The presented mechanism of LDT of *Alternaria* spores to Poland is based on the analysis of three selected LDT episodes. As mentioned in the Results section, the other episodes identified followed a very similar pattern in terms of length and direction of transport and source area. Therefore, we believe that the presented LDT mechanism is characteristic for the transport of *Alternaria* spores from the Pannonian Plain to Poland. In addition, given the vast area of the Pannonian Plain, the very high concentrations of *Alternaria* spores in this area, and the prevailing wind directions, we can assume that the LDT of spore is fairly common throughout the season (not only in September and October). However, because locally-released spores cannot be distinguished from LDT spores (at least without molecular analysis) it is extremely difficult to determine the frequency of this phenomenon. Finally, we cannot exclude that some post-seasonal increases in the concentration of *Alternaria* spores observed in Poznań result from phenomenon other than LDT, such as re-suspension of spores and agricultural practices. Locally, these processes may also boost the concentration of spores in the air.

### 4.2. Survival of Alternaria spores during LDT

Because of their minute size, and a high surface/volume ratio, airborne spores are largely exposed to external conditions, and many fungal spores are short-lived and highly susceptible to desiccation and UV radiation during atmospheric transport (Golan and Pringle, 2017; Gregory, 1973). *Alternaria* spores appear however to be one of the more resistant and well adapted to LDT, mainly due to increased pigmentation and wall structure (Rotem and Aust, 1991). *Alternaria* spores are thick-walled and contain a large amount of melanins (red, brown and black), that have been considered to confer tolerance to UV radiation (Kawamura et al., 1997; Kheder et al., 2012; Magyar et al., 2016). On the other hand, laboratory experiments (Mitakakis et al., 2003) showed that exposure of *Alternaria* spores to sunlight for one day reduced the proportion of spores able to germinate by 20%, while two days exposure dramatically affects the spore germinability (by 95%). Although, due to the methods used in this study (i.e. spore collection and counting procedures) we were unable to determine whether the spores were alive, dead, or had a reduced viability after LDT in the atmosphere but it can be assumed that the vitality of the spores should not be greatly reduced due to the <1 day estimated transport time. Stakman et al. (1923) who collected *Alternaria* spores from an altitude of 1000 to 3000 m observed that they germinated readily. In addition, the thick cloud cover as well as the presence of other particles in the air, e.g. dust, also provides additional protection of the spores from radiation (Gregory, 1973; Griffin et al., 2001; Parnell et al., 1998). At transport altitude, i.e. around 2000–3000 m, temperatures are markedly lower than on the ground level (−6.5 °C per 1000 m) and it is believed that such conditions are preservative rather than lethal. Many species of fungi will survive in a resting condition longer at the temperature found in the upper air than they will at ground-level (Gregory, 1973). Apart from sharp temperature fluctuations, which may potentially destroy the walls of the spore or denature its DNA (Parnell et al., 1998), temperature during LDT transport should not adversely affect the survival of the spores. Other factors that may potentially impact on spore condition are atmospheric turbulence, instability, and increased wind speed. During atmospheric disturbances, such as storms, broken *Alternaria* spores have been found in air samples (Pulimood et al., 2007), suggesting their susceptibility to mechanical damages. In general, wind speed increases with altitude (Hahmann et al., 2020), which can result in spore fragmentation. Presumably, the amount of broken spores may be related to both the duration and general conditions of atmospheric transport, however, this phenomenon has not been studied so far. Overall, we suspect that most of *Alternaria* spores (except for the fragmented ones) transported from the Pannonian Plain and deposited in Poland should be physiologically viable and be able to infect plants.

*Alternaria* spores transported during September–October have the potential to infect some farmed vegetables (e.g. carrots, potatoes, cabbage) or sugar beet (*Beta vulgaris*) whose harvest date is in the autumn. All the plants mentioned are susceptible to *Alternaria* spore infection (Khan et al., 2019; Thomma, 2003), and although the number of LDT *Alternaria* spores is probably too low to cause serious plant damage, some risk of infection nonetheless exists. For instance, the spread of plant disease induced by LDT fungal spores other than *Alternaria,* has been previously reported with respect to such fungal pathogens as coffee leaf rust (*Hemileia vastatrix*) or sugarcane rust (*Puccinia melanocephala*) (Brown and Hovmøller, 2002). Apart from direct infection, *Alternaria* spores deposited on the ground can overwinter in the soil or decaying plant debris (Thomma, 2003) and become a source of infection in the next growing season. The transport of airborne spores over long distances can be of great importance in the epidemiology of plant diseases, especially when new pathogenic races or fungicide-resistant strains develop and are spread across or between continents (Magyar et al., 2016).

### 4.3. Allergenic potential of Alternaria spores during LDT

Besides being an important plant pathogen, *Alternaria* spores are among the most potent triggers of allergic reactions in subjects sensitized to fungal spore allergens (Fukutomi and Taniguchi, 2015). The incidence of *A. alternata* sensitization within atopic patients varies between 3.6 and 39.4% depending on the climatic zone and the population tested (Heinzerling et al., 2009; Simon-Nobbe et al., 2008). Contrary to spore viability, it seems that UV radiation does not strongly influence the allergenic potential of *Alternaria* spores. Mitakakis et al. (2003) showed that both UV light (wavelength of 254 nm) and three days' exposure to simulated sunlight did not statistically affect allergen release from *Alternaria* spores. Grewling et al. (2019b) investigated the release of the main allergen of *A. alternata* spores, Alt a 1, in Poznań (Poland) during the sporulation season. The analysed period included data from 18 to 19 September 2014, i.e. Episode II in this study. *Alternaria* spores collected at this time contained considerable amounts of Alt a 1 (higher than the seasonal mean) (Grewling et al., 2019b). Taken together, both studies suggest that *Alternaria* spores transported from distant sources are still immunoreactive, i.e. they contain and can release allergenic proteins. Consequently, such LDT *Alternaria* spores, even dead or dormant, may pose a risk to *Alternaria*-sensitized subjects living far from the place of spore release.

### 4.4. Alternaria spores and other airborne biological particles

In the two examined episodes, *Ambrosia* (ragweed) pollen grains were observed in the air with a similar behaviour as *Alternaria* spores suggesting that these two types of bioaerosols were transported together. *Ambrosia* sp. is an extremely widespread invasive plant in the Pannonian Plain (Essl et al., 2015; Skjøth et al., 2019; Smith et al., 2013), although no stable ragweed populations were documented in Western Poland for the periods covered in this study. The presence of ragweed pollen in the air (especially, at night and in the early morning as it was observed in this study) is therefore a good indication that the incoming air masses have originated from areas highly infected by ragweed (Kasprzyk et al., 2011; Smith et al., 2008; Stach et al., 2007). The transport of ragweed pollen from the Pannonian Plain to Poland was previously described in detail, highlighting the typical atmospheric routes of air masses between the source and receptor areas and describing the synoptic conditions favourable to LDT (Bilińska et al., 2017; Grewling et al., 2016; Šikoparija et al., 2013; Smith et al., 2008). The concomitant occurrence of ragweed pollen and *Alternaria* spores has been linked to both the agricultural nature of the habitats in which they occur and similar weather conditions facilitating pollen and spore release (dry, warm and windy days) (Grewling et al., 2019a). Furthermore, ragweed can also be a host plant for *Alternaria*, as shown by Fehér (2013) who isolated *Alternaria* from different organs of *Ambrosia* (e.g. flowers and seeds) and observed adhered and germinated spores on the plant.

In the source area, i.e., the Pannonian Plain, other spores, especially *Cladosporium*, *Epicoccum* and *Stemphylium* are also common in air samples characterized by high quantities of *Alternaria* spores and *Ambrosia* pollen grains (Magyar, 2005). These fungi are typical members of 'dry weather airspora' (xerospores), having similar meteorological preferences in spore dispersal to *Alternaria*. Common features are hydrophobic and echinate surface and melanine content (Magyar et al., 2016). We suppose that these fungi can be also transported with the air masses carrying *Alternaria* and ragweed pollen. This is a potential focus of further study, where the presented modelling approach can be implemented. It is worth emphasizing that HYSPLIT model was predominantly used for tracking air mass movement and particle dispersion related to the atmospheric transport of various air pollutants, including pollen grains, volcanic ash, Saharan dust and anthropogenic air pollutants (Bogawski et al., 2019; Grewling et al., 2019a, 2019b; Šikoparija, B. 2020; Bihałowicz et al., 2021; Paez et al., 2021). Our study shows that this methodology can be successfully used to determine the sources and pathways of fungal spore transport in the atmosphere complementing the previous research in this area (Fernandez-Rodriguez et al., 2015; Sadyś et al., 2015; Grinn-Gofroń et al., 2021).

The investigation of several bioaerosols together can be useful in detecting peculiarities in airborne behaviour of certain particles. For instance, during the episode of 2014, two distinct peaks in *Alternaria* spore concentration were recorded, which suggests that *Alternaria* spores originated from two different sources. The first peak in *Alternaria* spore concentrations (between 16:00–20:00 on 18 September 2014) concurs with the typical diurnal pattern of airborne *Alternaria* spores recorded in Poznań. In addition, no ragweed pollen was recorded at this time and corroborates the hypothesis that *Alternaria* spores were released from local areas without ragweed populations, such as Central Poland. In contrast, elevated levels of *Ambrosia* pollen were noted during the second peak that occurred between 06:00–10:00 on 19 September 2014. This suggests that LDT from ragweed-infested areas had occurred, in this case from the Pannonian Plain. This was further supported by the results of back trajectory and particle dispersion analyses. The results of this study show that it is always worth paying attention to unusual and surprising objects present in the samples as they can markedly help in the data interpretation.

## 5. Conclusions

This study analysed the potential episodes of long distance transport of airborne *Alternaria* spores from the Pannonian Plain to the lowlands of Poland using a dense network of aerobiological monitoring stations, air-mass trajectory and dispersion modelling, and in-depth analysis of synoptic conditions. The nature of atmospheric fungal spore transport was characterized taking into account the period of occurrence, time of arrival, transport duration, and exact source location. To sum up, we showed that in the investigated LDT episodes, *Alternaria* spores were transported at least 600 km from the source area located in the north-western part of the Pannonian Plain. Some of the *Alternaria* spores were deposited in western Poland, although it can be concluded that the *Alternaria* spores could have been transported much further north by air masses, even as far as the Baltic countries. The examples presented in this study of *Alternaria* spores transported from south-east Europe to the north, resembles the LDT of ragweed pollen grains. These different bioaerosols seem to follow similar “atmospheric super highways”, in that particles released from the cauldron of the Pannonian Plain are able to travel northward, bypass the highest peaks of the Carpathians, break through the natural depressions in the Sudetes and eventually move into the lowlands of Poland. The identification of such atmospheric super highways can help us to better assess the risk of fungal spores (and other bioaerosols) for natural ecosystems, agricultural crops and susceptible human populations.

## Author contribution statement

All authors contributed significantly to the preparation of the manuscript. LG, MD, KCh, AG-G, NI, IK, MW, JL, BM-W, DM, VR, MB, MM, KP-W, AS-R, OR, JS, and BS collected and analysed local fungal spore data, took part in writing the manuscript, reviewed and edited its subsequent versions. The air-mass back trajectory analysis and dispersion modelling, synoptic and weather conditions analysis, statistical analysis and data interpretation, as well as preparing the final version of the manuscript were performed by LG, JG, AS, BS, CAS, MS, PB. Formulation of research problem and developing a research concept was done by LG, PB, MS, CAS and BS.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

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