



Live pine pollen in rainwater: reconstructing its long-range transport

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Abstract Raindrops brim with pollen even when there is no ambient local pollen. How does this nonlocal pollen get inside rain? The likely answer is long-range transport beneath or inside clouds. To test this hypothesis, we captured rain-delivered pollen on Ocracoke Island, NC, USA over a 12-day interval before local pine pollen release then reconstructed its trajectory and its atmospheric exposure conditions. Findings were as follows: four rain episodes yielded a total of 632 pollen grains of which 6.7% germinated. To find pollen sources, we first identified pollen-releasing forested areas using a predictive heat sum equation for each rain episode. Next, we constructed the backward trajectory for air parcels carrying rain-delivered pollen from those forests using the MLDP atmospheric transport and dispersion model. Nonlocal sources were located at distances up to 300 km from Ocracoke Island and distances lessened with each successive episode. Below-cloud transport time was 8 and 17 h for Episodes A and B, respectively. Pollen grains were exposed to harsh atmospheric conditions

during below-cloud transport, yet some grains still germinated. Atmospheric turbulence patterns changed for each episode, so distance from pollen source was poorly correlated with pollen transport time. Pollen germination was not closely correlated with either distances or transport time. In-cloud transport was more likely for pollen sampled during Episodes C and D. Pine pollen, although rarely allergenic, brings fresh insights into how atmospheric events can trigger human respiratory distress.

Keywords Aerobiology · Bioprecipitation · Long-range transport (LRT) · Long-distance dispersal (LDD) · Bioaerosols · Primary atmospheric bioaerosol particles (PBAPs) · Atmospheric dispersion model · Thunderstorm asthma

1 Introduction

Nearly a century ago, Busse (1926) reported finding pine pollen inside raindrops for four successive days although no local ambient pollen was present. Some of his rain-delivered pollen later germinated. So what brought this nonlocal pollen? The likely answer is long-range transport. Long-range transport has since been well-documented for pollen, fungal spores and other bioaerosols (e.g., Lanner 1966; Raynor et al. 1974; Aylor et al. 1982; Isard and Gage 2001; Aylor 2003; Mohanty et al. 2017).

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Even so, long-range transport as a source of allergenic particles has been overlooked in weather-induced asthma studies (Table 1). Weather-induced asthma refers to thunderstorms and weather fronts which trigger mass respiratory attacks in urban areas (Table 1). So far, these atmospheric models have focused on local allergens rather than pollen supplied by long-range transport. Here, we explore this using pine pollen as a model system.

Rarely allergenic, pine pollen is plentiful and easy to identify after long-range transport (Campbell et al. 1999). This type of pollen ($d = 40\text{--}70$ microns) retains its two-eared or bisaccate shape during transport (Schwendemann et al. 2007), has long-lasting buoyancy in air and water alike (Williams 2008) and makes a huge seasonal contribution to atmospheric aerosols (Williams and Després 2017). Pine pollen is a coarse bioaerosol, part of the size-defined portion known as primary biological aerosol particles (PBAPs) (Jäenicke 2005).

1.1 Schematic for long-range transport of pollen

How we hypothesize long-range transport for nonlocal pollen is shown in Fig. 1. Upon release, a fraction of pollen is vertically updrafted into the upper atmosphere where it concentrates in the planetary boundary layer (PBL) or higher (Mandrioli 1984; Westbrook and Isard 1999). Once aloft, pollen is transported by either or both below-cloud and in-cloud processes. Note that long-range transport does not adhere to the same assumptions as long-distance dispersal (LDD) (Katul et al. 2006) which is confined to micro-scale transport processes. Rather, long-range transport occurs at meso- and macroscale distances. Ascending pollen, retaining no concentration gradient, tends to be grouped inside air parcels (Lanner 1966; Raynor 1974) and thus rarely adheres to the well-mixed condition. Large quantities of pine pollen are transported in this way for hundreds or thousands of kilometers from the source (Campbell et al. 1999). Long-range transport of pollen is subject to complex atmospheric phenomena. Its trajectory typically shows a poor correlation between time and distance. Shorter distances can take

Table 1 A comparative analysis of weather models for predicting acute respiratory distress based on different assumptions about how pollen (and other bioaerosols) is transported

Model	Components	Description	Reference
Rain model	Downdrafts Inflows Wind Rain		Knox (1993)
Outflow model	Downdrafts Inflows Wind, not rain 80-km radius	Surface winds sweep bioaerosols into a downdraft and its outflows	Marks et al. (2001) Marks and Bush (2007)
Updraft model	Updrafts Cloud base, CCN Downdrafts Outflows Wind, not rain	Updrafted bioaerosols become hydrated, delivered to surface by downdraft and its outflow	Taylor and Jonsson (2004)
Mesoscale weather model	Mesoscale variables influencing outflows Wind, not rain 5 to 100 km distance	Air parcel energy (DCAPE), microburst wind speed index (MWPI), wind gust index (GUSTEX)	Andrew et al. (2017) Grundstein et al. (2017)
Frontal asthma	Trough of barometric pressure concentrates bioaerosols	Abrupt weather change to high humidity forces pollen rupture into subpollen particles (PM ₁₀ , PM _{2.5})	Robichaud & Comtois (2019)

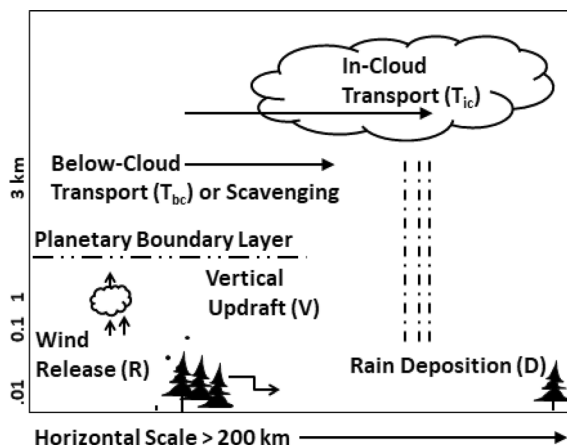


Fig. 1 Atmospheric schema for below-cloud versus in-cloud transport. Pollen is released (R) by gusting winds, updrafted vertically (V) and then transported beneath cloud base (T_{bc}) or inside clouds (T_{ic}). One or both transport paths can result in rain deposition (D)

more or less time (Raynor et al. 1974, 1983). Studying long-range transport of pollen is made possible with the combined use of biological and meteorological tools (e.g., Mohanty et al. 2017).

1.2 Vertical updrafting

Roughly 10–40% of pollen has been detected high above the forest canopy (see review Williams and Després 2017). This includes pollen at altitudes up to 2–3 km above ground level using LiDAR and at altitudes over 5 km using aircraft. Dense birch pollen concentrations were detected above 2-km altitudes in Alaska, USA, using LiDAR (Sassen 2008) and similarly, pollen clouds rose up to 2 km between 1200 and 1400 h daily in South Korea, using LiDAR (Noh et al. 2013). Tree pollen concentrations ride on sea breezes along the US Atlantic coast at around 1.4 km in altitude, forming large, dense plumes (Raynor et al. 1974). Pollen is transported in plume-like concentrations which tend to be condensed due to surface inversions. Inversions refer to a dry warm temperature layer above the PBL. Surface inversions, typical of coastal areas, are important because they cap upward dispersion of pollen (Raynor et al. 1974). Inland studies show similar findings: pine pollen also concentrates in the PBL in the Southern Great Plains, USA (Westbrook and Isard 1999), and above in Wyoming, USA (Mandrioli 1984).

1.3 Long-range transport processes and particle delivery

As mentioned, long-range transport of pollen has strong experimental support, historical and recent (Isard and Gage 2001). Other notable examples include *Betula* spp. pollen detected across the Baltic Sea (Hjelmroos 1991), *Ephedra* spp. pollen from the American Southwest found in Canada (Cambon et al. 1992) and exotic *Casuarina* pollen from Florida that arrived in Albany, NY after 20–24 h (Raynor et al. 1983). Pine pollen has also been detected above the Arctic Circle's tree line (e.g., Campbell et al. 1999). Inland, *Juniperus ashei* pollen was transported from the US Southern Great Plains to eastern Canada in three days (Mohanty et al. 2017). Below-cloud pollen is eventually scavenged by falling precipitation and returns to the earth's surface (Miquel 1883; Gregory 1961 p. 153; McDonald 1962). However, pollen's response to harsh atmospheric exposure during its long-range transport has not yet been directly measured, relying instead on laboratory studies.

Most atmospheric exposure work in laboratory simulations uses a variety of protocols (e.g., Diehl et al. 2001; Bohrerova et al. 2009; Pummer et al. 2012; Williams 2013; Hader et al. 2014; Steiner et al. 2015; Fröhlich-Nowoisky et al. 2016). One innovative approach is to simulate actual radiosonde data in the laboratory. This study predicted cold wet atmospheric conditions kill pine pollen (Bohrerova et al. 2009). The other laboratory studies measure how pine pollen responds to immersion freezing, a cloud ice process which accounts for 85% of cloud ice nucleation events. This was the case for pollen from six pine species. Pollen was still intact after immersion freezing assays and a fraction of pollen still germinated (Williams 2013). This particular laboratory study aligns with Busse (1926).

In this study, we test the long-range transport hypothesis from Busse (1926) using a mesoscale landscape experimental layout at the North Carolina Outer Banks described elsewhere (Williams 2010, 2020). This required (1) separating local from nonlocal pollen sources within a genus, (2) distinguishing below-cloud from in-cloud transport and (3) deducing pollen's response to atmospheric conditions during high-altitude transport. Distances between a pollen source and its rain delivery field were determined using a two-step method: finding pollen-

releasing forests using heat sum equations (HSEs) and then testing whether backward trajectory from an atmospheric dispersion model overlaps with that forested area. If so, forward trajectory was used to verify backward trajectory results.

2 Methods and materials

Rain-delivered pollen was sampled on Ocracoke Island during four rain episodes occurring over the 10 days before local pine pollen release; then, its germination was tallied. For two rain episodes, we could reconstruct transport distances and transport duration from nearest forests releasing pollen. From this, each pollen grain's atmospheric exposure could be made explicit for the below-cloud case.

2.1 Study organism

Pine pollen has been a well-documented tracking system for coarse bioaerosols for decades (see reviews in Williams 2009; 2010). Here, we make use of the natural range of *Pinus taeda* which spans 10 degrees of latitude across 13 US states on either side of the Mississippi River Valley. *Pinus taeda* is the predominant pine species of the southeastern USA, occurring over a total land area of 368,038 km² (Al-Rabab'ah and Williams 2002). Of this, over 228,023 km² occurs east of the Mississippi River Valley and of this eastern range, 41.5% is concentrated in South Carolina, Georgia and Florida (Al-Rabab'ah and Williams 2002). The extensive range of *Pinus taeda* overlaps with close relatives within its New World hard pine subsection *Austroales* and these include *Pinus palustris*, *Pinus serotina*, *Pinus echinata*, *Pinus elliotii*. All produce pollen grains which are too similar to be distinguished at the species level.

Note too that a narrow latitudinal band of *Pinus taeda* reproduces at a time. In Florida and Texas, *Pinus taeda* sheds pollen in February but farther north in South Carolina, pollen shed occurs by mid-March. In North Carolina, pollen shed is usually complete by mid-April. At each latitude, pollen is abruptly released. Day 1 is the peak pollen release day. More pollen is then released over the following 14–21 days, initially at high concentrations ranging from 4000 to 40,000 grains m⁻³ (Blush 1986).

2.2 Experimental layout

Rain-delivered pollen was sampled at the west-facing edge of the science pier of the North Carolina Center for the Advancement of Teaching (NCCAT) on Ocracoke Island (35.115°N 75.989°W) which is part of the North Carolina Outer Banks in the Atlantic Ocean (Fig. 2). Ocracoke Island, which lacks native *Pinus taeda* forests, is separated by the Pamlico Sound from a coastal mainland transect composed of over 35,000 ha of mature pine plantations (Fig. 2; Williams 2010). Ocracoke Island's atmospheric description during peak pollen release includes the diurnal PBL heights and surface inversion heights. Pine pollen captured on this Atlantic barrier island is released from over 35,000 ha of nearby coastal mainland *Pinus taeda* plantations located across the Pamlico Sound (Williams 2010, 2020).

2.3 Pollen sampling on Ocracoke island

Four rain episodes were grouped from rainfall from March 31 to April 12 (Julian dates¹ 90, 91, 94, 95, 102) during the 12 days before peak pollen shed at the nearest pine forests on the North Carolina mainland, which was April 11 (Julian date 101). Rain episodes were characterized using North Carolina's meteorological infrastructure: weather stations, radar and upper-air stations (Fig. 2; Williams 2010, 2020). Rain sampling was done using a plastic autoclave tray (0.5 m × 0.5 m × 10 cm) measured at hourly intervals or longer. Added to the sample was a sucrose-based blue aniline dye (5 µl per 100 ml rainwater) which has no effect on germination (Williams and von Aderkas 2011). Rain was sieved through 25-micron mesh fuel filters; then, pollen was plated on 0.5% Difco Bacto agar in Petri plants at 28 °C for 48 h before scoring.

2.4 Experimental controls for local pollen

Control-Air 1 (O) was pollen captured from wind using the Burkard air sampler model (Spiral Biotech, Advanced Instruments Inc., Norwood MA) which holds one agar-filled Petri plate. Each sample was run

¹ This is expressed on Eastern Standard Time. If expressed on UTC, then sampling took place on Julian dates would be 91, 93, 94, 95 and 102.

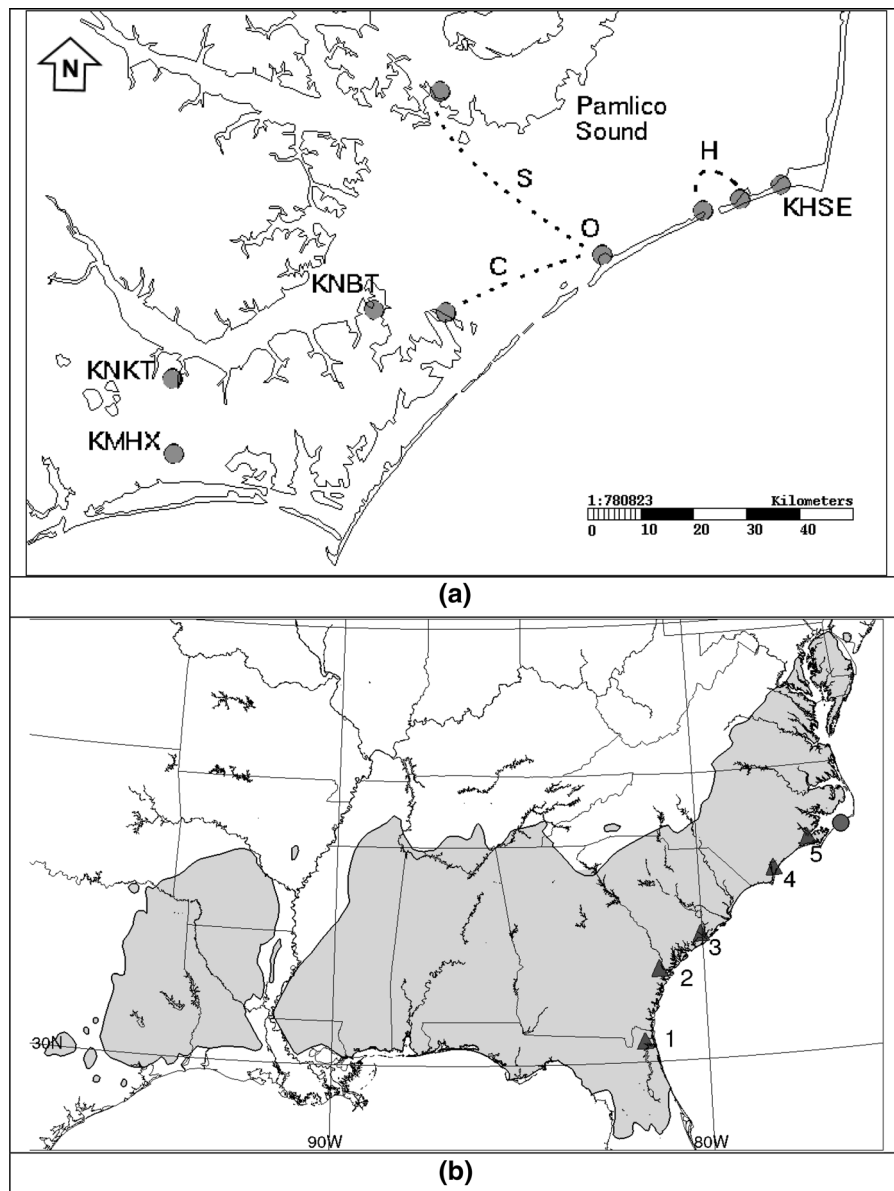


Fig. 2 Geographical landmarks for this study: **a** Pamlico Sound area with locations of Ocracoke (O), the ferry routes where spore samplers were installed (coded H: Ocracoke-Hatteras; C: Ocracoke-Cedar Island; S: Ocracoke-Swan Quarter), the weather stations of Billy Mitchell airport (KHSE), Marine Corps Air Station Cherry Point (KNKT), Piney Island (KNBT), and the Morehead City radiosounding station (KMHX); **b** *Pinus*

taeda range is represented by the light-gray shaded area; **c** weather stations providing data for heat sum equation are represented by gray triangles: (1) Jacksonville FL, JAX, (2) Savannah GA, SAV, (3) Charleston SC, CHS, (4) Wilmington NC, WMO, and (5) Cherry Point-Havelock, NC, MCAS. Ocracoke Island pollen sampling is the gray circle

for 15-min intervals at the same NCCAT pier location where rain pollen was captured, O = Pier for 0331-Rain. Control-Air 2 (S,C,H) was pollen captured from wind along the Pamlico Sound ferry routes on the round trip between Ocracoke Island and the mainland,

also using the spore sampler (Fig. 2). This wind control ran along three transects, with dates and cardinal directions as follows: 0403-Rain, 0404-Rain, 0405-Rain, 0409-Air, 0412-Air, Rain; S = Ocracoke-Swan Quarter ferry: WNW-SES transect for 0408-Air,

0412-Fresh, 0414-Air; C = Ocracoke-Cedar Island: SW-NE transect 0401-Air, 0407-Air and H = Ocracoke-Hatteras: N-S transect 0404-Air. Control-Air 3 was fresh pine pollen shed by trees in coastal mainland forests at the Swan Quarter ferry dock on April 12 (Fig. 2).

2.5 Tracing nonlocal pollen sources, their transport distances and atmospheric exposure

2.5.1 Identify pollen-releasing pine forests using heat sum predictive equation

Potential pine pollen sources could be located by latitude using a heat sum equation (HSE) to determine where pine pollen release was taking place along the US Atlantic Coast during a given rain episode. This is possible given that pollen release along the south-to-north latitudinal gradient within the species range can be accurately predicted using a HSE (Boyer 1978; Katul et al. 2006; Williams 2008) adopting a start date of January 1, 2013, a threshold heat accumulation set at 55°F and abrupt pollen release on day 1 near a threshold value of 636 h. Daily temperature data for HSE came from six weather stations along the coast including the primary station KNKT, Marine Corps Air Station at Havelock-Cherry Point (Fig. 2a).

2.6 Simulating atmospheric transport and dispersion for pine pollen

Meteorological data. Next, meteorological data required to drive the atmospheric dispersion model came from the operational Global Environmental Multiscale (GEM), a numerical weather prediction (NWP) model developed by the Canadian Meteorological Centre (CMC) of the Meteorological Service of Canada (Côté et al. 1998a, 1998b). For this study, the regional configuration (Caron et al. 2015) was used, which consisted of a grid over North America with a uniform horizontal resolution of 0.09° (approximately 10 km) and 58 terrain-following vertical levels. Meteorological fields at 6-h intervals (valid at 00, 06, 12 and 18 UTC) from March 28 through April 13, 2013, were used.

2.7 Atmospheric dispersion modeling

The CMC's Lagrangian stochastic particle dispersion model MLDP (*Modèle Lagrangien de Dispersion des Particules*) was used to simulate the transport and dispersion of the pollen grains in the atmosphere. This atmospheric transport model is used for operational support during emergencies requiring forecast plumes of volcanic ash, nuclear radiation, and toxic chemicals. Details on model formulation, application, and validation cases can be found in D'Amours et al. (2015).

Dry pine pollen has a settling velocity of 2.1 cm s^{-1} which was used in the simulations (Williams 2008), and a unit emission was used per run to characterize the source term. Simulations in backward and forward modes were performed. Backward atmospheric dispersion modeling tracks the ensemble of air parcels backward in time, prior to their arrival at Ocracoke. The resulting tracer concentrations from the backward atmospheric dispersion model are known as the source receptor sensitivity (SRS) coefficients (Wotawa et al. 2003) or transfer coefficient matrix (TCM) (Draxler and Rolph 2012). The SRS indicates the amount of air transported from a given region of the atmosphere into the sampler where the concentrations are measured and are expressed in the form of dilution factors in units of m^{-3} . The SRS was calculated for the layer 0–100 m above the ground to represent the layer where the pollen could have been initially emitted. Five million particles were used for each simulation, ensuring that the SRS values, averaged over a 1-h time step, are calculated with an adequate number of Lagrangian particles. Since the backward dispersion modeling only considers meteorological information and simulates the physical processes of atmospheric transport and diffusion, multiple areas can be associated with the potential sources at different times, meaning that several solutions coexist when finding the possible source areas. Thus, backward modeling results were coupled with the HSE in order to constrain geographically the phenology of pollen shedding as a function of the latitudinal gradient of temperature.

Hypothetical pollen sources from areas with high-density pine forests (Prasad and Iverson 2003) were chosen for the area pinpointed by HSE. In order to represent the transport of pollen from nonlocal sources, the initial vertical layers over Ocracoke

where Lagrangian particles were distributed were set in function of the PBL and the vertical extent of the humid layer from the atmospheric soundings of the nearby Newport station (MHX, WMO ID: 72,305). When the backward simulations succeeded in identifying possible source regions of pollen at near-ground level, then forward simulations were performed to confirm the validity of backward simulation results and to evaluate the extent of potential pollen clouds released during rain episodes at Ocracoke.

3 Results

3.1 Rain-delivered pollen captured in four episodes

A total of 632 intact pine pollen grains were collected at Ocracoke Island, of which 6.7% germinated later (Fig. 3). Hourly pollen counts were roughly 10 to 50 pollen grains per hour for April 4 (Fig. 4). About 30% of all rain-delivered pollen in this study was captured on March 31 well before local pollen release (Table 2). Four rain episodes (A-D) delivering pine pollen were characterized (Table 2). The backward atmospheric dispersion simulation was run by episode. The sampling periods where the pollen counts were very low and not contiguous with the other collection times were excluded of the groupings. As a result, excluded were April 1 at 1405–1505 UTC (pollen count = 1) and April 13 at 0055–0110 UTC (pollen count = 3).

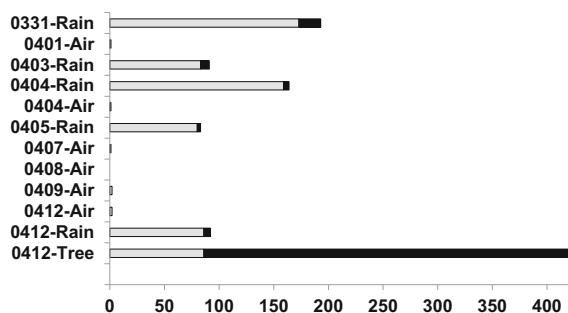


Fig. 3 The number of pine pollen grains captured during this study. No ambient pine pollen (AIR, TREE) was present before or after pollen was sampled (RAIN) during four precipitation episodes at Ocracoke Island, NC, for March 31–April 1 (Episode A), April 3 (Episode B), April 4–5 (Episode C), and April 12 (Episode D). Germinating pollen counts shown in black

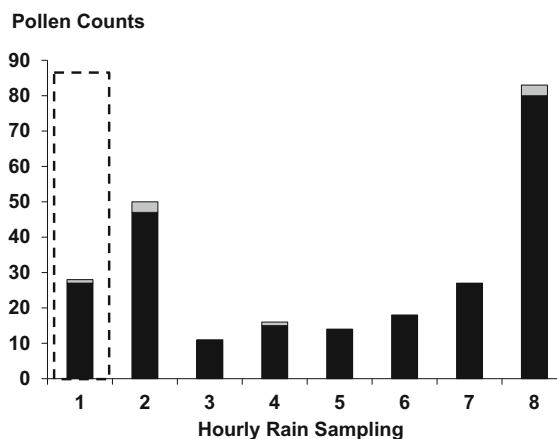


Fig. 4 Hourly pollen data collection on April 4 for Episode C. Sample 1 = 1500–1515 h, 2 = 1715–1815 h, 3 = 1815–1915 h, 4 = 1915–2015 h, 5 = 2015–2115 h, 6 = 2115–2209 h, 7 = 2210–2300 h, 8 = 2300–0700 h EDT. Grey indicates number of germinating pine pollen grains. Dotted line shows the expected outcome if falling raindrops had simply scavenged local ambient pollen suspended over Ocracoke

3.2 Detecting local pollen from nearby coastal mainland and Ocracoke Island

Control-Air 1 had no windborne pollen that was collected on Ocracoke Island before or after all precipitation events. Control-Air 2, a ferry sampling on the Pamlico Sound (Figs. 2, 3), showed no pine pollen from dates April 1 to April 9. Control-Air 3 measured no pollen shedding on the mainland pine trees. No local pollen release was predicted based on the Boyer (1978) heat sum accumulation; heat sum hours from the KNKT weather station had only reached 481 and 513 heat sum hours, respectively, during the March 31 storm and April 4 storm. By April 11, nearby pine forests were releasing pollen as predicted by the HSE and Control-Air 3 showed fresh pollen released from two Swan Quarter trees which had 88% germination and 79% germination on April 11–12 (Fig. 3).

3.3 Tracing long-range transport of pollen using backward atmospheric dispersion simulations

3.3.1 Episode A

This episode featured rain that fell overnight between March 31 and April 1, coming from showers located east of a cold front associated with a low-pressure

Table 2 Pollen sampling on Ocracoke Island is grouped into four rain episodes (shown inside shaded cells) where actual sampling time (Eastern Daylight Time, EDT) is shown

Date/time (local time, EDT)		Date/time (UTC)		Pollen count	Episode
2013-04-01	Overnight	2013-04-01	Overnight	193	A
	1005–1105		1405–1505	1	
	0830–0945	2013-04-03	1230–1345	91	B
	1500–1515		1900–1915	28	
	1715–1815	2013-04-04	2115–2215	50	C
	1815–1915		2215–2315	11	
	1915–2015		2315–0015	16	
	2015–2115		0015–0115	14	
	2116–2209		0116–0209	18	
	2210–2300		0210–0300	27	
	2300–0700		0300–1100	83	
	1000–1100	2013-04-12	1400–1500	31	D
	1320–1400		1720–1800	51	
	1510–1600		1910–2000	15	
	2055–2110	2013-04-13	0055–0110	3	
Total				632	

system located over Pennsylvania on April 1, which later moved northeastward along the East Coast. Images of reflectivity and total precipitation from the radar KMHX (Newport/Morehead) show that a band of precipitation moved west to east and that precipitation over Ocracoke occurred between approximately 04 and 06 UTC on April 1.

This timing is confirmed by surface observations at KHSE, the weather station closest to Ocracoke (Fig. 2a), which indicated around 1 mm of rainfall accumulation, an amount consistent with the multi-sensor precipitation estimator (MPE) values (between 0.25 and 2.5 mm), a combination of radar data and rain gauge observations. Episode A had, on average, meteorological conditions which featured westerly winds of 10 to 20 km/h, a temperature of 14 °C, a relative humidity of 90% and a cloud base at 2700 m above ground-level. By analyzing the closest radiosonde readings at Newport, the PBL height and vertical extent of the humid layer were estimated to be 630 m and 4000 m, respectively.

Given the motion of the precipitation band, it seems likely that the rain-collected pollen came from south (Table 3). Indeed, this is consistent with the HSE prediction of pine pollen release between Charleston, SC and Wilmington, NC, near the Waccamaw National Wildlife Refuge, roughly 300 km southwest of Ocracoke Island.

The SRS from the backward simulation representing the potential source area of pollen released at near-ground level is presented in Fig. 5. A potential pollen source is just south of Wilmington on April 1 at 00UTC, which appears to be inside the *P. taeda* range (Fig. 5a). However, HSEs indicate that predicted pollen release at that location was not expected until April 3 to 4 (Table 3), which is inconsistent with the solution given by the dispersion model. For March 31 at 22UTC, the SRS covers northern coastal and inland part of South Carolina (Fig. 5b), and this is consistent with HSE which predicts that pollen release in coastal areas in this area would be between March 10 and April 4.

Consequently, the overlap between the backward simulation and the HSE points to nonlocal pollen from the northernmost coastal South Carolina. Having been transported for about 300 km, pine pollen in Episode A had an atmospheric transport duration of 7 to 10 h.

3.3.2 Episode B

Rain-delivered pollen was collected from brief precipitation on April 3 morning. This was part of an eastward-moving surface trough located at the eastern edge of a vast high-pressure system centered over the Great Lakes area. Radar KMHX indicated an isolated, elongated area of precipitation moving from west to east, with precipitation falling likely between 1140

Table 3 Potential nonlocal pine pollen sources sampled on Ocracoke, NC, USA, in 2013 on March 31–April 12

Location	Latitude (degrees)	Longitude (degrees)	Distance from Ocracoke Island rain sampling (km)	Predicted pollen release based on heat sum for 2013
Ocracoke, NC	35.115	– 75.989	0	–
Swan Quarter, NC	35.406	– 76.329	45	April 12
Cherry Point, NC	34.900	– 76.880	85	April 12
Wilmington, NC	34.270	– 77.900	198	April 3–4
Charleston, SC	32.899	– 80.041	447	March 10–11
Savannah, GA	32.128	– 81.202	585	February 25
Jacksonville, FL	30.494	– 81.688	739	February 9

This was determined using the predictive heat sum equation (Boyer 1978) for local pollen release dates. Southerly latitudes of the *Pinus taeda* range shed pine pollen days or weeks before coastal North Carolina

and 1410 UTC, while pollen was being collected between 1230 and 1345 UTC.

This narrow precipitation band did not pass over the KHSE weather station (Fig. 2a) and MPE indicated no precipitation. However, based on radar precipitation products, it is estimated that around 1 mm of rain fell over Ocracoke area during this episode. Average weather conditions featured northeasterly winds were 20 km/h gusting to 40 km/h, a temperature of 9 °C, a relative humidity of about 50% and a cloud base at 1800 m. Based on radiosonde data, the estimated PBL height was 100 m while the vertical extent of the humid layer was at 4000 m.

Similar to Episode A, this Episode B rain-collected pollen had a likely origin from south of Ocracoke where the HSE predicts pine pollen release near the Cape Fear River Basin in southernmost North Carolina near Wilmington.

About 8 h prior to pollen collection on Ocracoke, on April 3 at 06 UTC, the potential pollen source from the backward simulation was north of Ocracoke, over the Alligator River National Wildlife Refuge (NC) where no *P. taeda* pollen was yet being released (Fig. 5c). Further in the backward simulation, on April 2 at 18 UTC (Fig. 5d), the SRS includes the coastal region between Wilmington and Ocracoke, consistent with HSE predictions.

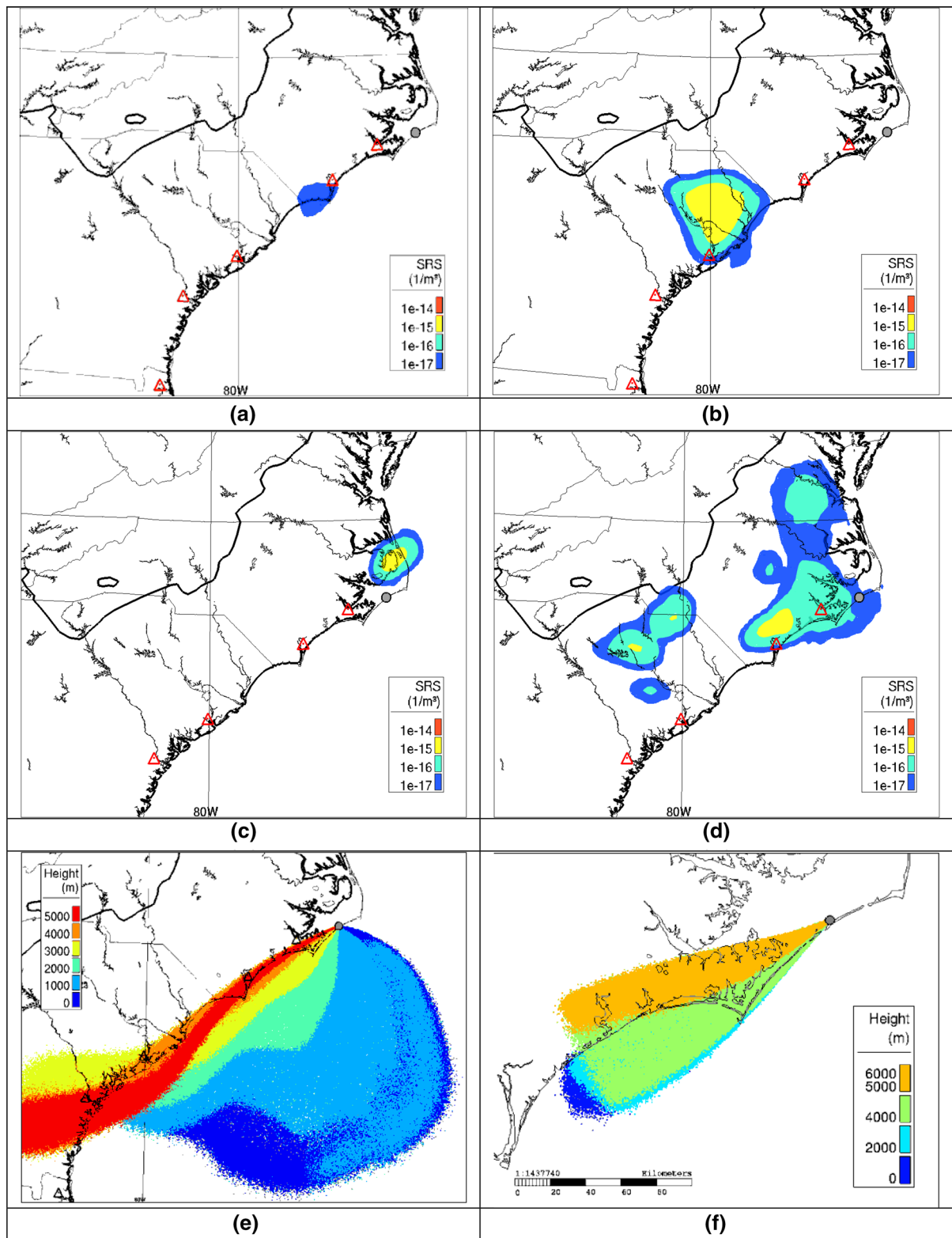
3.3.3 Episode C

This episode had the longest rainfall due to stratiform precipitation associated with a warm front extending from a low-pressure system. This system was located over coastal South Carolina on April 5 before moving

northeastward. Precipitation lasted for 12 h between April 4 at 19UTC and April 5 at 7 UTC, based on radar data and surface observations at KHSE. The MPE values show 25 to 38 mm rainfall over Ocracoke, which was consistent with accumulated rainfalls at KHSE (28 mm) and at KNBT (32 mm).

Rain bands were carried by winds aloft from the southwest where *P. taeda* pollen was shedding in Wilmington area (Table 3). Average surface observations at KHSE indicated east to southeast winds at 40 km/h, a temperature of 14 °C, a relative humidity over 90% and a cloud base around 1000 m with values as low as 400 m. The PBL height and the vertical extent of the humid layer were estimated to be 400 and 5500 m, respectively.

Here too predictions from HSE pointed to southerly North Carolina, near the Cape Fear River Basin, but backward simulation failed to identify near-ground level sources at locations and times consistent with the pollen-releasing forest areas indicated by the HSE. In order to evaluate what could have been the possible atmospheric path reaching Ocracoke, Fig. 5e shows the instantaneous locations and heights of the Lagrangian particles on April 4 at 22 UTC. The only pollen at altitudes higher than 4 km at that moment was transported on southwesterly winds from coastal NC to Ocracoke for a duration of 3–4 h. Radiosonde data support this. However, the atmospheric dispersion model could not simulate the uplift process that transported pollen from near-ground level to an altitude of 4 km or more for Episode C.



◀ **Fig. 5** Results from the backward atmospheric dispersion simulations starting at Ocracoke. Panels (a) to (d) show near-ground level (0–100 m above ground level). Source receptor sensitivity (SRS) for Episode A on (a) April 1, 2013, at 00UTC, (b) March 31 at 22UTC, and for Episode B on (c) April 3 at 06UTC, and (d) April 2 at 22UTC. Panels (e) and (f) show the Lagrangian particle heights for (e) Episode C on April 4 at 22UTC and (f) Episode D on April 12 at 18UTC. Ocracoke Island pollen sampling locations (gray dot), weather stations providing data for the heat sum model (triangles) and *P. taeda* range (black bold line) are also shown

3.3.4 Episode D

Episode D was associated with pre-frontal bands of precipitation east of a sweeping cold front extending from a complex and large area of low-pressure over the southern part of the Great Lakes area on April 12. Strong convective cells were moving eastward, as indicated by radar data. Rain showers lasted from 1400 to 1920 UTC. Based on MPE values, rainfall ranged from 6 to 19 mm over Ocracoke area, which was consistent with rainfall of 11 to 19 mm measured at KHSE and KNBT, respectively. Mean surface conditions at KHSE were southwest winds of 20 km/h, a temperature at 18 °C and a relative humidity at 90%. Cloud base varied widely, from 150 to 3300 m, with an average value of 1200 m. Based on radiosonde data, the PBL height and the vertical extent of the humid layer were 300 and 6500 m, respectively.

HSE model predictions showed pollen-releasing forests near New Bern, NC, and Havelock, NC, in the vicinity of the dense pine stands in the Croatan National Forest (Table 3). This area is southeast of Swan Quarter, NC (location of Control-Air 3). Any nonlocal pine pollen from this area would have been briefly transported in the atmosphere for a short distance before being brought down or scavenged by raindrops.

Similar to Episode C, the atmospheric dispersion model could not identify a source located at near-ground level. Indeed, as depicted in Fig. 5f which shows the locations and height of the Lagrangian particles on April 12, 2013, at 18UTC, the backtracked particles at altitudes below 5 km were over the peninsula southwest of Ocracoke, extending from Morehead City to Cedar Island National Wildlife Refuge, where there is few *P. taeda* stands. This suggests that the only pine pollen transported at

heights between 5 and 6 km had to be located over the pine forests of Croatan National Forest, the closest origin of rain-delivered pollen.

3.4 Pollen exposure during atmospheric transport

Waccamaw National Wildlife Refuge and the Cape Fear River Basin could be resolved as likely pollen sources for Episode A and Episode B, respectively. Both areas are convergent for HSE and atmospheric dispersion simulations, so these are the better choices for examining pollen exposure during atmospheric transport to Ocracoke.

For Episode A, the mean backward displacement from the Waccamaw National Wildlife Refuge required 8 h of atmospheric residence time (Fig. 6). For Episode B, the Cape Fear River Basin source was a shorter transport distance which required 17 h, over twice as much transport duration. Therefore, we conclude transport distance is poorly correlated with transport duration.

Episode A's backward trajectories had particles at an altitude of 1000 m over Ocracoke. These had reached a maximum value of 1550 m after 5 h near the Waccamaw National Wildlife Refuge (Fig. 7). This was similar for Episode B where particles originated at about 1250 m above Ocracoke and stayed at this altitude for 8 h before gradually descending toward near-ground level over the Cape Fear River Basin.

However, Episodes A and B had different meteorological conditions during their respective trajectories. First, Episode A's particles from Waccamaw National Wildlife Refuge South Carolina were transported farther and faster, at a mean wind speed of 57 km/h, compared to Episode B's particles transported from Cape Fear River Basin North Carolina at a shorter distance going a mean wind speed of only 13 km/h. Second, for Episode A, particles were transported beneath the cloud base inside a warmer and more humid atmosphere than for Episode B. Also, Episode A had a lower mean vapor pressure (0.56 kPa) compared to Episode B (1.14 kPa), yet in both cases, a fraction of pine pollen germinated after capture.

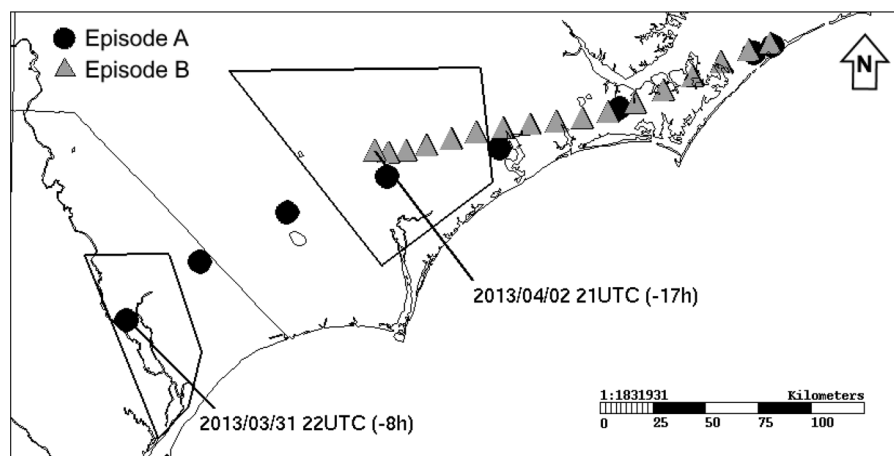


Fig. 6 Simulated hourly locations of the average position of the clusters of Lagrangian particles in backward mode departing from Ocracoke to the hypothetical source areas of Waccamaw

National Wildlife Refuge, SC (Episode A) and Cape Fear River Basin, NC (Episode B). The polygons depict the areas considered for the source regions

3.5 Forward simulations confirming the validity of backward atmospheric dispersion results

Using Waccamaw National Wildlife Refuge and Cape Fear River Basin as pine pollen sources (Fig. 6), forward simulations were next performed with 10^6 Lagrangian particles released during the time ranges identified from the backward simulations (Table 4) and initially uniformly distributed over the entire pollen source areas in a layer of 100 m height above ground level.

The resulting plumes, computed in the layer 1000–1500 m AGL which corresponds to the traveling altitudes of the pollen cloud over Ocracoke (Fig. 7), are presented in Fig. 8. In both cases, it is validated that the pollen cloud passes over Ocracoke. These findings verify that pollen clouds released from the two sources could have been scavenged by raindrops falling over Ocracoke Island.

Thus, we report that long-range transport could explain how pollen got into raindrops even though no local pollen was being released, just as Busse (1926) reported (Tables 1–4). Our findings, as summarized in Table 4, support (1) rain-delivered pollen captured in four episodes, (2) no local ambient pollen was detected on Ocracoke or nearby coastal mainland forests, (3) pollen exposure during atmospheric transport was mild to harsh yet 30% of all rain-delivered grains germinated after 8 h transport from 300 km away in South Carolina. Forward simulations confirmed backward atmospheric dispersion findings.

Note too that coarse bioaerosols are transported swiftly for long distances beneath storm clouds or inside storm clouds. Here, we offer new meteorological methods for modeling thunderstorm asthma and other weather-induced respiratory events. This finding also suggests that sources of allergen particles could be located far from a storm's deposition site.

4 Discussion

4.1 Findings are consistent with Busse (1926)

Pine pollen was transported via winds below-cloud and in-cloud for 8–17 h for distances up to 300 km from Ocracoke. In our study, after pollen was scavenged by falling raindrops, a fraction was still capable of germination in all four episodes. This experiment corroborates findings reported for Busse (1926) and laboratory-based immersion freezing assays of pine pollen (Williams 2013). If pollen was hydrated prior to the immersion assay, then its germination showed a steep decline afterward. By contrast, dry pollen shows little change in its germination rates after harsh immersion freezing exposure (Williams 2013).

Pollen grains did not germinate inside raindrops (Busse 1926), and this was also our finding. Germination is slow for pine pollen, so we suggest that pine pollen may require more than 8 to 17 h at higher temperatures as well as hydration in a neutral pH (e.g., Pardi et al. 1996).

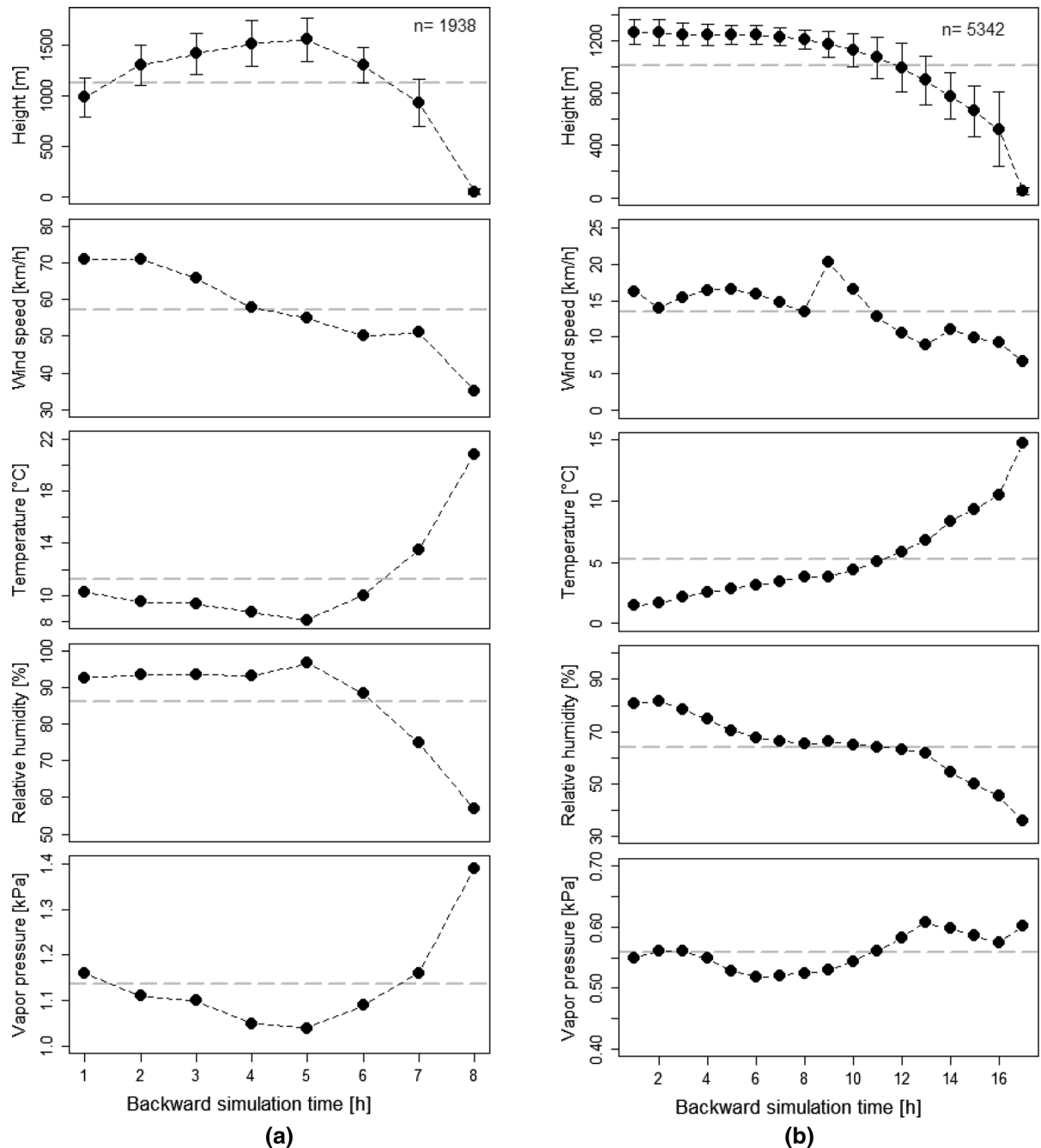


Fig. 7 Pollen grain exposure to atmospheric conditions during flight. Particle heights above ground level and meteorological fields computed from backtracking trajectory analysis of Lagrangian particles starting at Ocracoke at hour 0 and then traveling at near-ground level over *P. taeda* pollen hypothetical sources: **a** Episode A flight over Waccamaw National Wildlife

Refuge and **(b)** Episode B flight over Cape Fear River Basin. Values are computed from the mean location of particle clusters (Fig. 6). Gray-dashed lines indicate the average values over the trajectory simulations. The error bars in the upper panels indicate the standard deviation of the particle heights within the clusters, along with their size (*n*)

Table 4 Summary of findings for observed pine pollen sampling on Ocracoke Island and its simulated atmospheric transport path, conditions and duration by episode (Ep.)

Ep	Synoptic feature of rain event	Rainfall duration* [h]	Rainfall amount* [mm]	Resolved near-ground pollen emission**	Pollen atm. res. time** [h]	Date of possible pollen release** [UTC]	Possible source and distance from Ocracoke [km]	Mean pollen traveling altitude** [km]	Mean cloud base during rainfall* [km]	Assumed pollen traveling layer	Pollen count by episode	Germination rate (%)
A	Cold front	2	1	Yes	~ 7–10	2013/03/31 2030 ± 0230	WNWR ¹ (325)	1.1	2.7	Below-cloud base	193	10.4
B	Trough	2.5	1	Yes	~ 15–20	2013/04/02 2000 ± 0330	CFRB ² (200)	1.0	1.8	Below-cloud base	91	8.8
C	Warm front	12	30	No	~ 3–4	2013/04/04 2200 ± 0600	CFRB ² (200)	> 4	1.0	In cloud	247	3.2
D	Cold front	5	10–20	No	~ 1–2	2013/04/12 1530 ± 0230	CNF ³ (100)	5–6	1.2	In cloud	97	6.2

*from the observations (radar, MPE, weather stations)

**from the backward atmospheric dispersion simulations

¹Waccamaw National Wildlife Refuge, SC²Cape Fear River Basin, NC³Croatan National Forest, NC

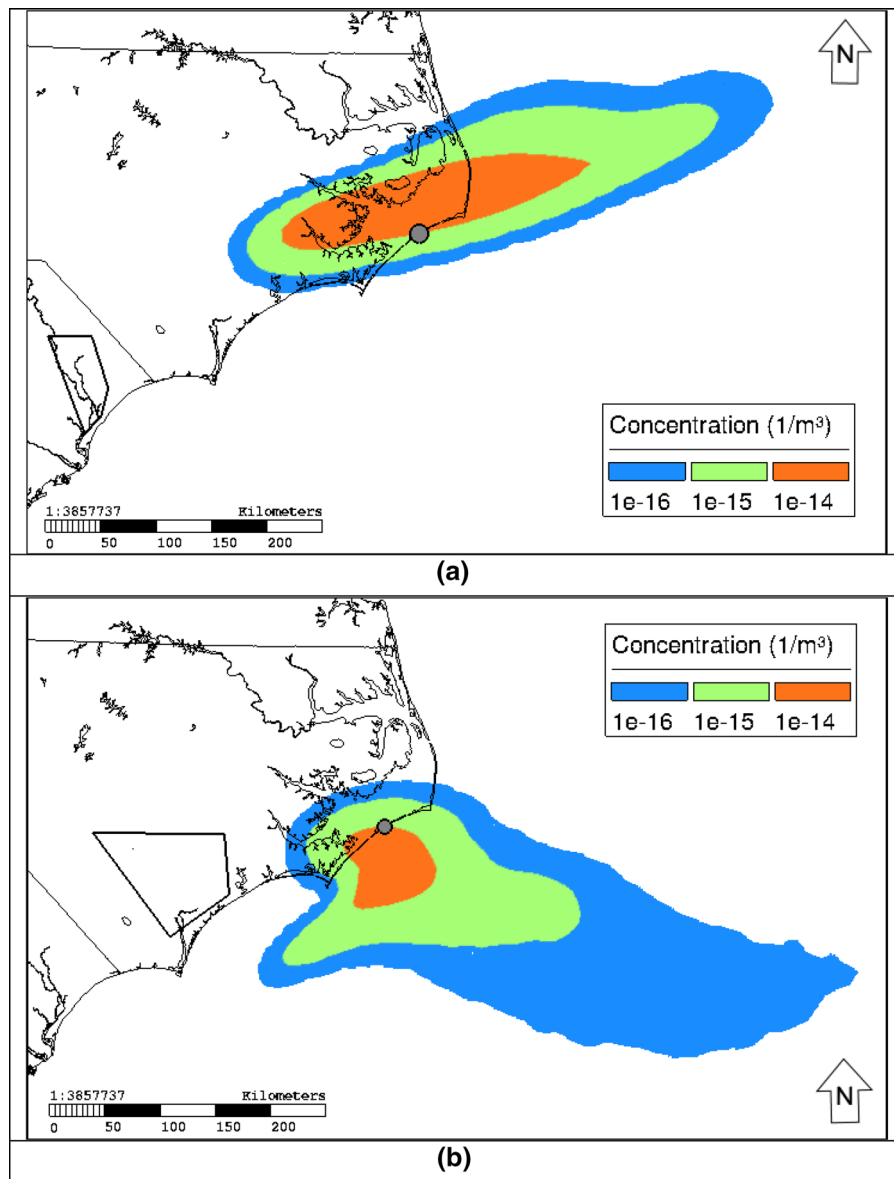


Fig. 8 Forward simulations using the hypothetical pollen source regions from Fig. 6. The panels represent the pollen ambient air concentration, expressed in terms of dilution factors,

in the layer 1000–1500 m AGL for the date and time when precipitation approximately started for (a) Episode A (2013/04/01 at 04 UTC) and (b) Episode B (2013/04/03 at 13 UTC)

4.2 Policy relevance to thunderstorm asthma

No thunderstorms brought pine pollen for Episodes A–D nor were asthma attacks measured. However, we do show how long-range nonlocal pollen can be transported across a robust variety of atmospheric phenomena before and during rain delivery even when no local pollen is present. These new methods and findings also suggest that pine pollen is a good

experimental model and that it can serve as a tracer bioaerosol.

4.3 Atmospheric dispersion modeling uncertainties

We offer three caveats and drawbacks to this study: spatial resolution, time scale and aerodynamics.

First, the NWP model horizontal grid resolution was of 10 km, meaning that surface properties are averaged and subgrid processes are parameterized (e.g., not explicitly resolved), such as convection. In the case of meteorological fronts and particularly in the case of active cold fronts, the updrafts that generate the clouds at small scale are much higher than depicted by the NWP model in which the vertical motion is averaged on its grid cells resolution. In addition, the parameterization of the convective boundary layer in MLDP is rather simple and does not integrate any convection scheme that redistributes the particles among the convective layer, as described in Forster et al. (2007). This could explain why the backward simulations failed to represent potential sources of pollen at near-ground level for Episodes C and D. Moreover, the sea breeze circulation, which influences the pollen dispersion (Raynor et al. 1974) and occurs at the Outer Banks (Williams 2020), is not always well-represented in our NWP model.

Second, the time resolution of meteorological input to the dispersion model was of 6 h, implying that meteorological data for 3D winds were interpolated to serve as input in MLDP. With the passage of weather fronts, especially with cold fronts where wind speed and direction can change rapidly, the interpolated values are subject to greater uncertainties.

Third, pollen settling velocity might have been different than the constant dry pollen settling velocity of 2.1 cm/s used here. Pollen grains are hygroscopic and thus hydrate easily so that its settling velocity is expected to change with higher relative humidity (e.g., Bunderson and Levetin 2015; Chen et al. 2019).

In closing, pine pollen was delivered by four rain episodes, each sourced by nonlocal forests south of Ocracoke Island, USA. To find sources by episode, we used a heat sum predictive model to find pollen-releasing forests in the *Pinus taeda* range and then applied backward atmospheric dispersion modeling approach to identify likely pollen sources.

This offers new methods for pinpointing allergen particles for weather-induced respiratory distress such as thunderstorm asthma.

Using these new methods, our key findings are that below-cloud transport could be inferred for Episodes A and B across transport distances up to 300 km. In-cloud transport could be inferred for Episodes C and D for transport distances up to 200 km from Ocracoke. Likely pine pollen sources were confirmed using

forward simulations. Using forward simulations, we deduced pine pollen's atmospheric residency to be 17 h or less. During residency, pollen grains experienced a wide range of atmospheric conditions during transport, including low vapor pressure deficits and low temperatures, yet it did not die. Some pollen grains were capable of germinating later, after capture as reported in the historical account given by Busse (1926). This and other field studies corroborate pine pollen's remarkable ability to endure immersion freezing exposure at high altitudes yet still germinate. Rain delivers live pine pollen from nonlocal sources.

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