

The first record of subtropical insects (Thysanoptera) in central Europe: long-distance transport of airborne thrips, applying three-dimensional backward trajectories

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- Abstract**
- 1 The present study reports the first occurrence and flight period of three species, namely *Scolothrips tenuipennis* zur Strassen 1965, *Frankliniella schultzei* Trybom, 1910 and *Zurstrassenia figuratus* zur Strassen, 1968 (Thysanoptera: Thripidae), in Hungary. A fourth, undescribed species belonging to the genus *Caliothrips* was also captured.
 - 2 The distribution area of these species is North Africa and it is hypothesized that they are transported to Hungary via long-distance air currents.
 - 3 Data for a suction trap are examined in South–East Hungary, in the 3-year period 2002–2004 from May to September. A three-dimensional back-trajectory analysis based on the Hybrid Single-Particle Lagrangian Integrated Trajectory (HYSPLIT) transport and dispersion model was performed for the observation days to determine the origin and path of air masses and evaluate of the possibility of long-distance transport of thrips species.
 - 4 Surprisingly, the analysis showed that only a few percent of the back trajectories originated or passed over North Africa. The results suggest that the captured thrips species could survive long-distance transport at low-level trajectories and establish new populations in Western Europe, the eastern part of Europe and Northern Central Europe, which together serve as source areas for the long-range transport of thrips to the target station.

Keywords *Frankliniella schultzei*, HYSPLIT model, long-distance dispersion, migration, *Scolothrips tenuipennis*, *Zurstrassenia figuratus*.

Introduction

Insect pests can cause serious damage with respect to vegetable production (Hummel *et al.*, 2002). For example, the western flower thrips *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), has become one of the insects that is the most difficult to control in the intensive agriculture of south-eastern Spain (Bielza *et al.*, 2008).

Many Thysanoptera species are widely spread and are capable of reaching new habitats and crops far from their source of origin

(Lewis, 1973). The airborne thrips species are habitually exposed to the wind (Mound, 1983). The recorded heights attained by species *Frankliniella tritici* at 3100 m and *Caliothrips phaseoli* at 1200 m (Glick, 1939) facilitate their spread over great distances in seasonal or prevailing winds. However, because flying thrips are unobservable beyond a few metres, their behaviour in the upper air is open to speculation. Thus, some long-distance dispersion might consist of alternate periods of wing beating in warm air and inert tossing in cool air, with final controlled orientation to vegetation and alighting (Lewis, 1997).

In studies, trajectory models may involve either backward or forward trajectories in time. The models demonstrate that the transport of particulates (being either physical or chemical

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particles, or bio-aerosols) is a fairly complex process. It involves extended vertical changes of the air masses that may cover long distances from the source to the target area in a short time interval. Dust and other aerosols have been applied several times as air mass tracers, both for studying long-range transport processes (Dimitriou & Kassomenos, 2014) and palaeoclimatological analyses (Bourgeois *et al.*, 2000). Some investigations have employed bio-aerosols to trace air masses and/or to detect source areas of given bio-aerosols, such as pollen (Cecchi *et al.*, 2007; Makra *et al.*, 2010; Paschalidou *et al.*, 2015), spore (Aylor *et al.*, 1982), virus (Li *et al.*, 2009) and insects (Carlson *et al.*, 1992). A joint search in Web of Science with keywords 'insect' and 'long-distance transport' produced 90 papers. Many of them include a trajectory analysis of the transport processes (Carlson *et al.*, 1992; Westbrook *et al.*, 1995; Dantart *et al.*, 2009; McLaren *et al.*, 2010; Sturtevant *et al.*, 2013; Lander *et al.*, 2014). Carlson *et al.* (1992) calculated the long-range transport of the potato leafhopper (*Empoasca fabae*) from the source region into Michigan with a nocturnal jet at an air pressure of 850, 900 or 950 mb, respectively. Westbrook *et al.* (1995) determined backward trajectories of different endpoints for noctuids aiming to predict long-distance dispersion and subsequent infestations by migratory pest insects. Bejarán *et al.* (2008) found that the mosquito *Ochlerotatus albifasciatus* (Diptera: Culicidae) is transported by wind to Buenos Aires. Dantart *et al.* (2009) studied the long-distance dispersal of *Cornifrons ulceratalis* (Lepidoptera: Crambidae: Evergestinae) into the northern Mediterranean. Kim and Sappington (2013) established that dispersal events of 640–740 km could be expected between boll weevil populations on a regular basis. Miao *et al.* (2013) analyzed the possible dispersion trajectories and distances of *Sitodiplosis mosellana* depending on the experimental location based on the Hybrid Single-Particle Lagrangian Integrated Trajectory (HYSPLIT)-4 model. Sturtevant *et al.* (2013) designed a high-resolution atmospheric model for budworm flight behaviour using air temperature, wind speed and precipitation data and produced detailed flight trajectories and deposition patterns. Eagles *et al.* (2013, 2014) used HYSPLIT to simulate the dispersion of *Culicoides* spp. from Indonesia, Timor-Leste and Papua New Guinea into northern Australia. Lander *et al.* (2014) investigated the explanatory power of a regional-scale wind-dispersed particle trajectory model for the invasive seed chalcid wasp *Megastigmus schimitscheki* (Hymenoptera: Torymidae) in France. However, so far, only one paper has dealt with the long-distance transport of thrips using trajectory calculations (McLaren *et al.*, 2010), in which probable trajectories were computed for New Zealand flower thrips (*Thrips obscuratus* Crawford) transported to Central Otago in the Spring using wind speed, wind direction and air temperature data collected at several meteorological stations, and then the departure conditions were characterized.

Several observations on long-distance dispersion of different insect species were described by McManus (1979). After reviewing the international literature, it was found that a large number of papers have been published so far that apply the HYSPLIT transport and dispersion model to detect the potential source areas of insects captured in the target area. Kedmi *et al.* (2010) found that winds are a major contributory factor for the long- and medium-distance spread of *Culicoides* borne viruses in Israel. Using HYSPLIT, Zhu *et al.* (2006) showed

that spring low-level jet streams are significantly associated with the intensity of *Myzus persicae* flight activity. Using HYSPLIT, Feng *et al.* (2007) constructed backward trajectories assuming that carabids moved at the same velocity as the wind. It was found that the flight speed of carabids generally exceeded the wind speed, especially in weak winds; furthermore, carabids flew with different flight speeds depending on the direction of the backward trajectories. Stefanescu *et al.* (2007) found a strong association between migration of *Vanessa cardui* from North Africa to southern Europe and synoptic-scale wind currents. Episodes of the massive northward migration within the species' flight boundary layer also coincided with winds originating from North Africa, suggesting a connection between low-altitude (observational) and high-altitude flights. Dantart *et al.* (2009) studied the long-distance dispersal of *Cornifrons ulceratalis* (Lepidoptera: Crambidae: Evergestinae) into the northern Mediterranean. They used HYSPLIT for the back-trajectory analysis of air masses at two different altitudes, which suggested that the moths most probably originated from an area located in Morocco and northern Algeria, where *C. ulceratalis* may be extremely abundant. Westbrook *et al.* (2011) used the HYSPLIT atmospheric dispersion model to simulate the daily wind-assisted dispersion of weevils from the Lower Rio Grande Valley of southern Texas and north-eastern Mexico. The dispersion model accurately estimated 71.8%, erroneously estimated 12.5% and linked 15.7% of capture and noncapture events. Their model simulations provided a temporal risk assessment over large areas of weevil reinfestation resulting from dispersion by prevailing winds. García-Lastra *et al.* (2012) used the HYSPLIT model to investigate whether infected *Culicoides* were introduced into Basque Country by winds from the infected areas of Southern Spain during 2007 and 2008, causing bluetongue as a vector-borne disease of ruminants. Kim and Sappington (2013) established that dispersal events of 640–740 km could be expected between boll weevil populations on a regular basis. Miao *et al.* (2013) calculated dispersion trajectories and distances of *S. mosellana* for the Hebei province in China using the HYSPLIT model. Eagles *et al.* (2013, 2014) used HYSPLIT to simulate the dispersion of *Culicoides* spp. from Indonesia, Timor-Leste and Papua New Guinea into northern Australia. Applying dispersion trajectories of HYSPLIT, Lander *et al.* (2014) proposed that wind is the most probable vector for the passive long-distance dispersion of the invasive seed wasp. Their findings confirmed that long-distance dispersion from source areas is a likely driver of the secondary expansion of invasive species.

Note that a single backward trajectory has a large uncertainty and is of limited statistical significance (Stohl, 1998). Trajectory position error is typically considered to be approximately 20% of the traversed distance (Stohl, 1998), although the statistical uncertainty will be substantially reduced when using a large number of back trajectories. However, we cannot use a large number of backward trajectories because we have only occasional samples for the study period. The reason for taking into account two back trajectories arriving at the heights of 500 and 1500 m above ground level (AGL) at the Hódmezővásárhely target station in Southern Hungary on the flight days is that hotter days are associated with more frequent, longer-lasting and deep convective plumes, potentially allowing more insects to be spread through the convective boundary layer, rising to heights

of up to 1–2 km above ground level (Bell *et al.*, 2013). We should add that three-dimensional (3D) back trajectories were selected because they are known to be more accurate than any other types of trajectories, including isentropic ones (Stohl & Seibert, 1998).

A large number of papers have been published so far on the long-range transport of insects. The present study aimed to identify key geographical regions as potential source areas of airborne invasive insects (thrips species) caught over the city of Hódmezővásárhely in Southern Hungary.

Materials and methods

Location

Hódmezővásárhely (46.42 N; 20.33 E) is a large settlement in south-eastern Hungary (Fig. 1). The area is characterized by an extensive flat landscape of the Great Hungarian Plain, namely the Pannonian Plain. Hódmezővásárhely is the lowest-lying city in Southern Hungary, with an average height of 77 m above sea level. Hódmezővásárhely (a city with the largest administrative area in Hungary) has 47 000 inhabitants. The climate of the city can be characterized by Köppen's Ca type (warm temperate climate) with relatively mild and short winters and hot summers (Köppen, 1931) (Fig. 1).

Data

A Rothamsted-type suction trap (Burkard Manufacturing, U.K.) was operated by the Csongrád county Plant Protection and Soil Conservation Service, at Hódmezővásárhely in South-East Hungary, in the years 2000–2005, from April to October. This suction trap is the only one in the area. It drew in 3000 m³ of air per hour at a height of 12 m. The diameter of the collecting tube was 20 cm. The collecting jar was changed daily in the morning at 0600 UTC (Coordinated Universal Time) during the experiment. The collected specimens were then preserved in 70% ethanol. Each of the Thysanoptera specimens examined was mounted on slides and they were identified according to zur Strassen's diagnostic keys (2003).

The data set consists of a 3-year period covering 2002–2004. In years 2002 and 2004, the first and last captures occurred on 2 May and 25 June, as well as on 25 September and 18 August, respectively. Furthermore, in the year 2003, only one thrips specimen was captured: on 21 August (*Caliothrips* sp.). Altogether, 51 flight days were detected in the above-mentioned 3-year period.

Methodology

Backward trajectories. Hegarty *et al.* (2013) evaluated three widely used Lagrangian particle dispersion models (LPDMs), namely the Hybrid Single-Particle Lagrangian Integrated Trajectory (HYSPLIT), Stochastic Time-Inverted Lagrangian Transport (STILT) and Flexible Particle (FLEXPART) models, with measurements obtained from a series of controlled tracer-release experiments called Cross-Appalachian Tracer Experiment (CAPTEX) and Across North America Tracer Experiment (ANATEX). The LPDMs were run forward in time driven by identical meteorological inputs from the North



Figure 1 Location of Hódmezővásárhely in Europe and Hungary (upper) and the urban web of the city with the position of the insect trap (●) (lower). [Colour figure can be viewed at wileyonlinelibrary.com].

American Regional Reanalysis (NARR) and several configurations of the Weather Research and Forecasting (WRF) model, and the simulations of tracer concentrations were evaluated against the measurements with a ranking procedure derived from a combination of four statistical parameters (Figure of Merit in Space, Probability of Detection, False Alarm Rate and Threat Score/Critical Success Index). A statistical evaluation showed that all three LPDMs had comparable ability in simulating the tracer plumes when driven by the same meteorological inputs, indicating that the differences in their formulations play a secondary role. The HYSPLIT transport and dispersion model was chosen by us in the present study (Draxler & Hess, 1998; Stein *et al.*, 2015) because this model had been successfully applied in previous studies for detecting the source area of insects captured at the target area (Bejarán *et al.*, 2008; Dantart *et al.*, 2009; Kedmi *et al.*, 2010; Westbrook *et al.*, 2011; García-Lastra *et al.*, 2012; Eagles *et al.*, 2013, 2014; Kim & Sappington, 2013; Miao *et al.*, 2013; Lander *et al.*, 2014), as well as for its application to the spread of aerosols of diseases of veterinary importance (Garner *et al.*, 2006).

To detect possible source areas of thrips species, backward trajectories of air masses for Hódmezővásárhely (Southern Hungary) were computed by using the Hybrid Single-Particle Lagrangian Integral Trajectory (HYSPLIT, version 4.8; <http://www.arl.noaa.gov/ready/hysplit4.html>; Draxler, 1996, 1999; Draxler & Hess, 1998; Draxler & Rolph, 2003; Stein *et al.*,

2015; Rolph, 2017) model, obtained from the U.S. NOAA National Center for Environmental Prediction (NCEP)/National Center for Atmospheric Research (NCAR) (<http://dss.ucar.edu/datasets/ds090.0/>).

In the present study, 4-day, 6-hourly 3D backward trajectories (three coordinates: φ , latitude; λ , longitude; h , height) arriving at 0000 UTC at heights $h = 500$ and 1500 m AGL were generated on the flight days and calculated every 6 h (http://ready.arl.noaa.gov/HYSPLIT_traj.php) to describe the horizontal and vertical movements of an air parcel arriving at Hódmezővásárhely. A back-trajectory analysis of 5 days in total was performed: they were partly the days that yielded the most catches (i.e. 28 June 2004; 26 July 2004; 28 July 2002; 17 June 2002) and partly a day with a typical North-African origin back trajectory (i.e. 5 August 2002). The 4-day period is a frequently used period for back-trajectory analyses in entomology (Stefanescu *et al.*, 2007; Dantart *et al.*, 2009).

The HYSPLIT model can calculate backward trajectories using three approaches, these being (i) based on vertical velocity fields, as well as (ii) isobaric and (iii) isentropic approaches. We used isentropic trajectories (where the potential temperature surface is constant) that are generated from the gridded meteorological fields of the Final (FNL) archive data (Draxler *et al.*, 2016). A height of 500 m AGL approximately corresponding to the 1000 hPa standard air pressure level, was selected because previous data from vertical-looking radar stations indicate that the maximum transport of migrant insects over Europe occurs around this height (Chapman *et al.*, 2003; Stefanescu *et al.*, 2007; Dantart *et al.*, 2009). A height of 1500 m AGL, approximately corresponding to the 850-hPa standard air pressure level was also selected because the layer from the ground up to this height forms the boundary layer with the main characteristics of strong turbulence in the lower troposphere (Atkinson, 1981; Stefanescu *et al.*, 2007). This layer is typically sensitive to cyclonic wave features and it is the approximate boundary between the surface wind regime and the free troposphere (Artz *et al.*, 1985). Moreover, a relationship between the 850-hPa wind direction and the prevailing weather patterns associated with the passage of cyclonic waves is well established (Dayan & Lamb, 2003).

Note that the draining of the trap occurred on the given day (including 0000 UTC), whereas the last day of the flight was the day before. With the choice of the 0000 UTC start time of the model run, the trap could catch insects for the whole 24-h period of the day before (Zhu *et al.*, 2006; Stefanescu *et al.*, 2007; Miao *et al.*, 2013).

The meteorological data used for the computation of the back trajectories were obtained from the NOAA NCEP/NCAR Global Reanalysis 1 project (<https://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.html>) and were downloaded by HYSPLIT. This reanalysis dataset comprised four parameters from NCEP Parameter Code Table 1, as well as 93 parameters from NCEP Parameter Code Table 2 (http://rda.ucar.edu/datasets/ds090.0/#metadata/grib.html?_do=y). The meteorological data have a spatial resolution of $1^\circ \times 1^\circ$ (approximately $100 \text{ km} \times 100 \text{ km}$) in latitude and longitude, as used in several studies (Hernández-Ceballos *et al.*, 2014, 2015; Rojo & Pérez-Badia, 2015).

To better understand the meteorology of the transport of thrips, 3D values of the ambient air temperature (K), downward solar

radiation flux (W/m^2), mixed layer depth (m), rainfall (mm/h) and relative humidity (%) were analyzed, along their transportation paths (<http://www.arl.noaa.gov/ready/hysplit4.html>).

Uncertainty in backward trajectories. Because a single backward trajectory has a large uncertainty (Stohl, 1998) (see the Introduction), when computing archive trajectories, the trajectory frequency option was selected (http://ready.arl.noaa.gov/HYSPLIT_traj.php) to achieve a greater certainty on the paths of the back trajectories. The trajectory frequency option will start a trajectory from a single location and height every 6 h, sum the frequency that the trajectory passed over a grid cell and then normalize the sum by using the total number of trajectories (<http://www.arl.noaa.gov/ready/hysplit4.html>). A trajectory may intersect a grid cell once or multiple times (with residence time options 1, 2 or 3) (trajectory frequency = $100 \times$ number of endpoints per grid square/number of trajectories).

Within the model parameter 'Vertical motion', we applied the isentropic trajectories option (where the potential temperature surface is constant), which are generated by the gridded meteorological fields of the Final (FNL) archive data (Draxler *et al.*, 2016) (<http://ready.arl.noaa.gov/hypub-bin/traj1.pl>). A height of 1500 m AGL, approximately corresponding to the 850-hPa standard air pressure level, was selected. The reason for selecting this level is that the layer from the ground up to this height is the boundary layer with the main characteristics of strong turbulence in the lower troposphere (Atkinson, 1981; Stefanescu *et al.*, 2007).

Concentration and dispersion. To determine atmospheric concentrations and dispersion, the model can be run in the 'puff' or 'particle' mode, or a combination of both. In the present study, the particle mode was chosen, which allows for the release of a fixed number of particles (Stein *et al.*, 2015). This mode permits the transport of particles with a mean wind speed and a random component to account for turbulence (Garner *et al.*, 2006). The particle source is simulated by the release of a set number of particles (evenly distributed between source sites, if there is more than one) over a specified duration. When concentration runs were performed, both 'dry' (gravitational) and 'wet' (rainfall) depositions were permitted (Eagles *et al.*, 2013).

When running the dispersion model, several parameters should be specified. The dispersion direction is forward, the latitude and longitude of the back-trajectory position should be stated; release top and top averaged layer are the same and, in every selected 6-h position up to 24 h back in time, they are the actual AGL height of the back trajectory, whereas release duration, total duration and averaging period are all set to 6 h. During modelling, the most important elements are the term and degree of emission. We chose 1 unit of mass as the release quantity that is produced by the pollutant source for 1 h. In other words, this means that, at given geographical coordinates, the dispersion of a unit emission of a fictitious source during unit time can be analyzed. Because the dry deposition value is unknown, we use 0.001 m/s as the default (<http://ready.arl.noaa.gov/hypub-bin/disp1.pl>).

Maps of trajectory frequencies and mass concentrations, as well as weather maps. Using the frequency option on the READY

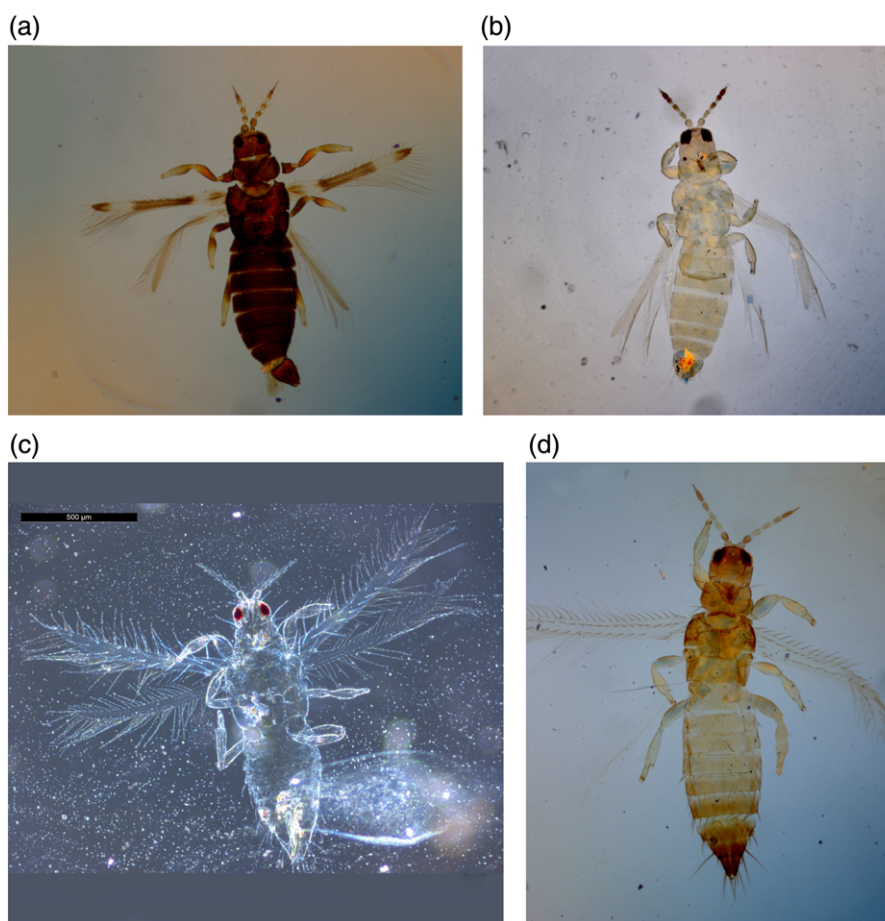


Figure 2 Thysanoptera species captured at Hódmezővásárhely: (a) *Caliothrips*, (b) *Zurstrassenia figuratus*, (c) *Scolothrips tenuipennis* and (d) *Frankliniella schultzei*. Scale bar = 500 µm. (Photos by Miklós Bozsó and Szilvia Orosz, 2016; National Food Chain Safety Office, Plant Health and Molecular Biology Laboratory, Budapest, Hungary.) [Colour figure can be viewed at wileyonlinelibrary.com].

website, maps of trajectory frequencies were generated for the height of 1500 m AGL to detect more reliable paths of the backward trajectories. Trajectory frequency on the map is interpreted as $100 \times$ number of endpoints per grid square/number of trajectories (<http://www.arl.noaa.gov/ready/hysplit4.html>).

Maps of averaged areal mass concentrations and also dispersion of thrips between 0 and 1500 m AGL were also prepared, integrating for the last 24-h period ending at 0000 UTC (i.e. the insect catching date) (<http://www.arl.noaa.gov/ready/hysplit4.html>).

In addition, to analyze the role of the actual weather in the migration of thrips, archive weather charts with sea level pressure maps, including high and low air pressure areas and weather fronts for the North-Atlantic–European region (UKMO-Bracknell-Bodenanalysen, from 27 January 1998 to present) were evaluated for the given days at 0000 UTC (<http://old.wetterzentrale.de/topkarten/tkfaxbraar.htm>). In addition, archive 850-hPa geopotential (gpm) [1 gpm (geopotential decametre) = 10 gpm (geopotential metre)] and air temperature (°C) maps for the North-Atlantic–European region (NOAA-CR20 and NCEP Reanalysis, from 1 January 1871 to the present) were also investigated (<http://old.wetterzentrale.de/topkarten/fsreaur.html>) (Draxler *et al.*, 2016).

According to Draxler *et al.* (2016), ‘Gridded meteorological data, on a latitude-longitude grid or one of three conformal (Polar, Lambert, Mercator) map projections, are required at regular time intervals’. Normally, the map projection is computed by the model automatically based upon the location and length of the trajectory (default projection). In the present study, we chose the default projection. However, some trajectory combinations may produce no maps or improperly scaled maps. In such situations, we may prefer to over-ride the default projection and try forcing a selection (Polar-, Lambert- and Mercator projections) offered by the model (Draxler *et al.*, 2016).

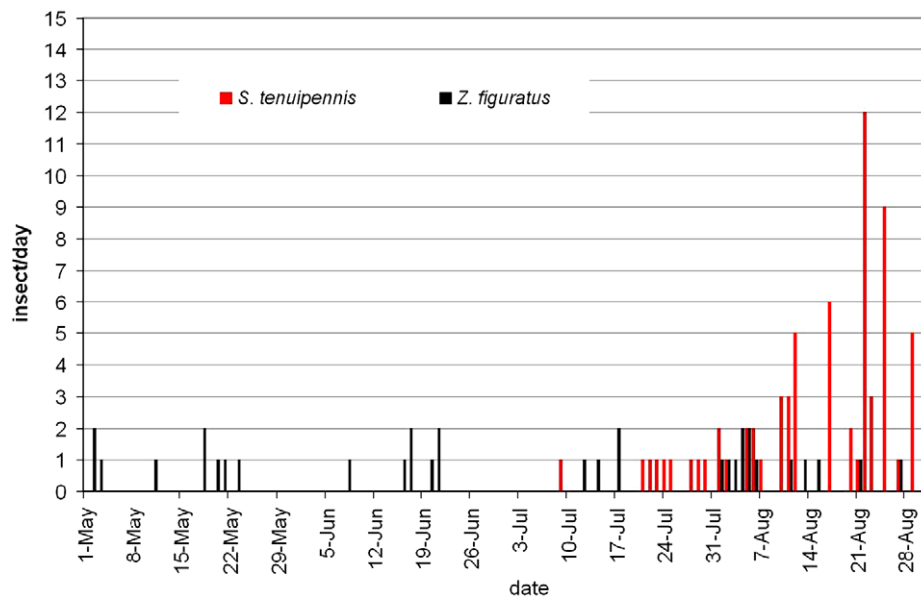
Results

Thysanoptera species captured by the suction trap

During the monitoring period, more than 40 *Thysanoptera* species were captured, including four species, namely *Scolothrips tenuipennis* zur Strassen 1965, *Frankliniella schultzei* Trybom 1910, *Zurstrassenia figuratus* zur Strassen 1968 and *Caliothrips* sp., that have not yet been reported over the study area (Fig. 2). The suction trap captured two male *Caliothrips* specimens that were very close or identical

Table 1 Statistical data for the *Thysanoptera* species captured from the air, Hódmezővásárhely, 2002–2004

Year	Number of monitoring days	Basic statistical parameters	<i>Caliothrips</i> sp.		<i>Frankliniella schultzei</i>		<i>Scolothrips tenuipennis</i>		<i>Zurstrassenia figuratus</i>	
			Male	Female	Male	Female	Male	Female	Male	Female
2002	230	Sum	0	0	0	0	0	68	8	25
		Maximum	0	0	0	0	0	12	1	2
		Number of catching days	0	0	0	0	0	26	8	21
2003	211	Sum	1	0	0	0	0	0	0	0
		Maximum	1	0	0	0	0	0	0	0
		Number of catching days	1	0	0	0	0	0	0	0
2004	214	Sum	1	0	2	1	0	0	0	3
		Maximum	1	0	2	1	0	0	0	1
		Number of catching days	1	0	1	1	0	0	0	3

**Figure 3** Seasonal flight activity of *Zurstrassenia figuratus* and *Scolothrips tenuipennis* caught by a suction trap in 2002. [Colour figure can be viewed at wileyonlinelibrary.com].

to *Caliothrips floridensis* Nakahara 1991 (B. G. Vierbergen, personal communication). *Caliothrips floridensis* has only been known from its female specimens so far. However, the male specimens of *Caliothrips* sp. cannot be identified at the species level without female specimens. No males of *S. tenuipennis* zur Strassen were found in the samples, whereas both sexes were present for the remaining two species.

The total number of the above-mentioned thrips spp. caught from the air was 68 for *S. tenuipennis*, 36 for *Z. figuratus*, three for *F. schultzei* and two for *Caliothrips* sp. (Table 1). The species occurred rarely in the air samples. The highest number was registered in 2002, when an almost continuous presence of *S. tenuipennis* was observed over 24 days, from 21 July to 29 August. However, the majority of *Z. figuratus* was observed in smaller numbers between 2 May and 17 July, in 2002 (Fig. 3).

Using the HYSPLIT transport and dispersion model and READY website, 4-day backward trajectories are calculated on the insect catching days, which indicate the place of origin of the insects, as well as the characteristics of the transported air

masses. The length of the back trajectories determined for this period is between 1014 and 2759 km for the 500-m arrival height, whereas it is between 940 and 2931 km for the 1500-m arrival height, respectively (Fig. 4a–e).

Caliothrips males were found on days with trajectories originating in the Atlantic biogeographical region (Normandy, Northern France). *Frankliniella schultzei* (both males and females) were caught on days when the trajectories originated from Poland. For these species, no back trajectories originating or passing over Africa were found. As for the other two species, the situation was more complex. Some trajectories were short, prevailing in Central Europe at low altitudes (<1500 m AGL). At the same time, long trajectories also occurred, although they did not refer clearly to the same source region. *S. tenuipennis* females appeared on days when the trajectories arrived from the east, south and north-west; passing over the Mediterranean (38%), the Steppic East-European (38%) and the Black Sea (23%) regions. However, the back trajectories were also present over the Atlantic area (27%). Back trajectories originating from North-Africa

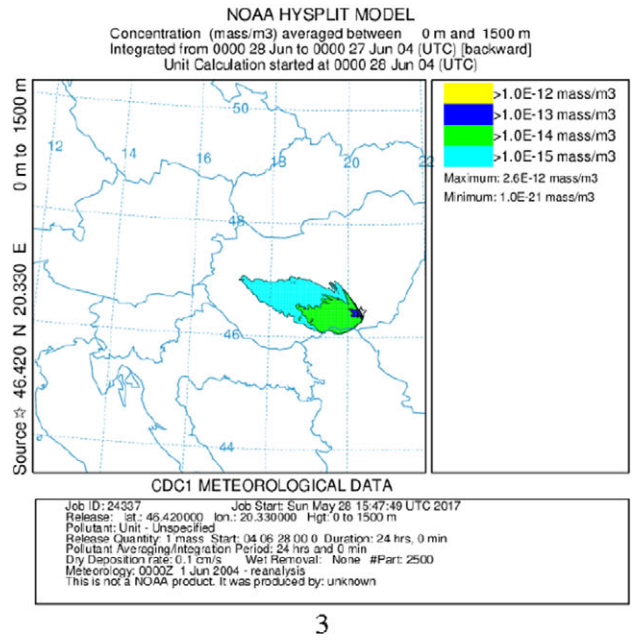
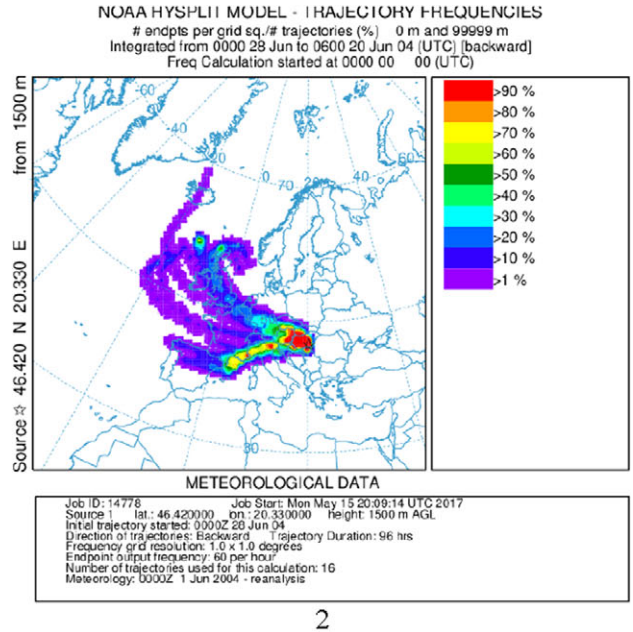
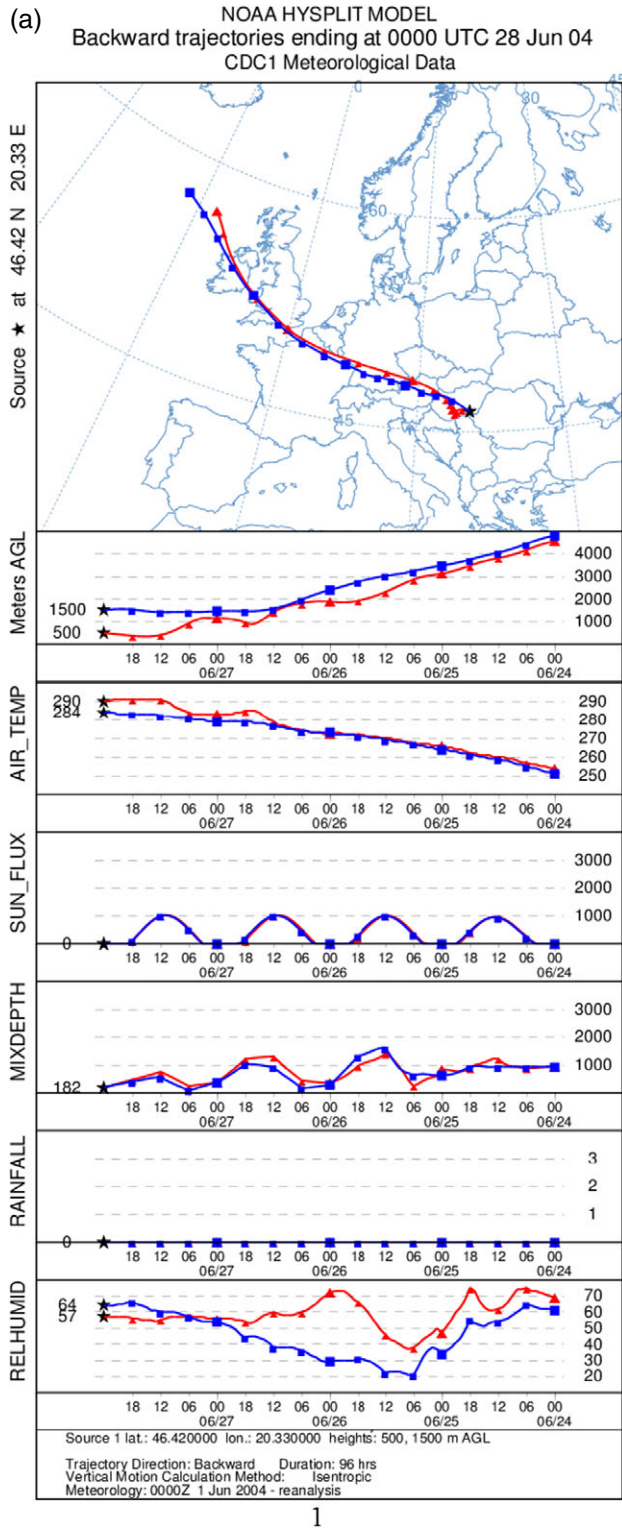


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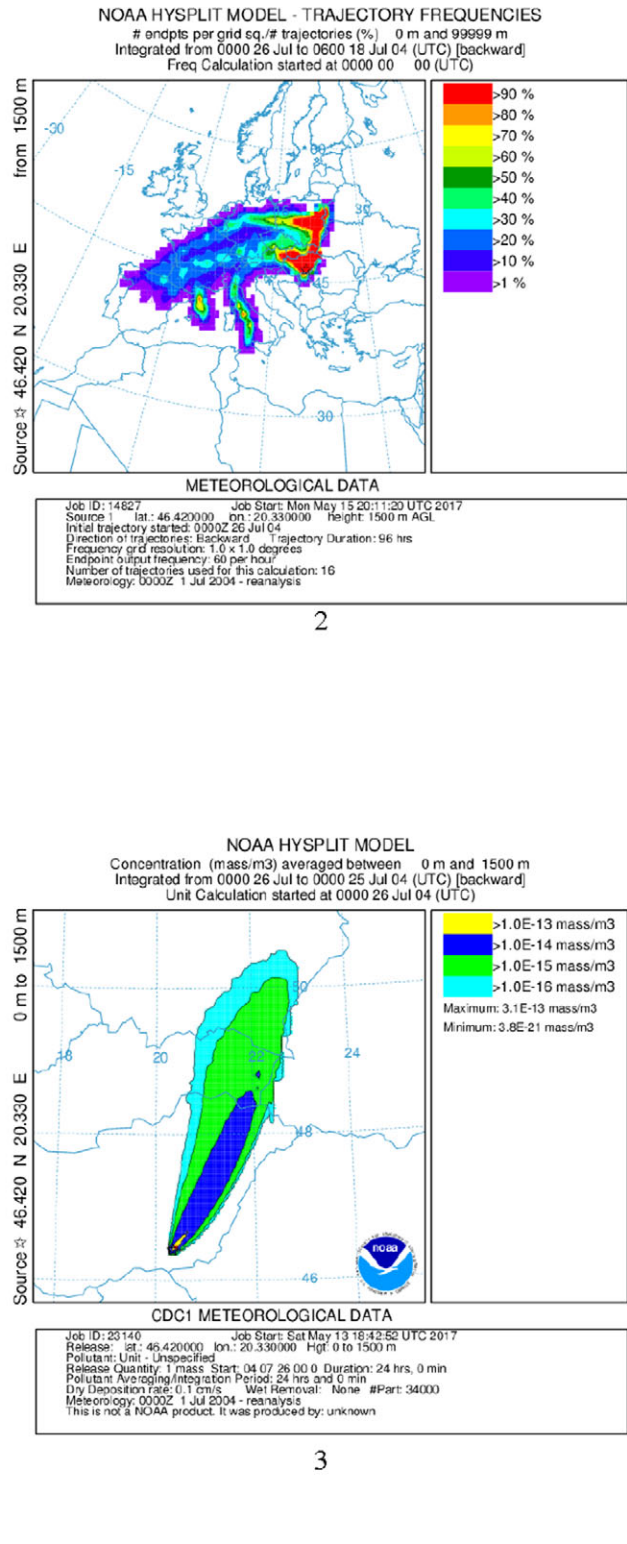
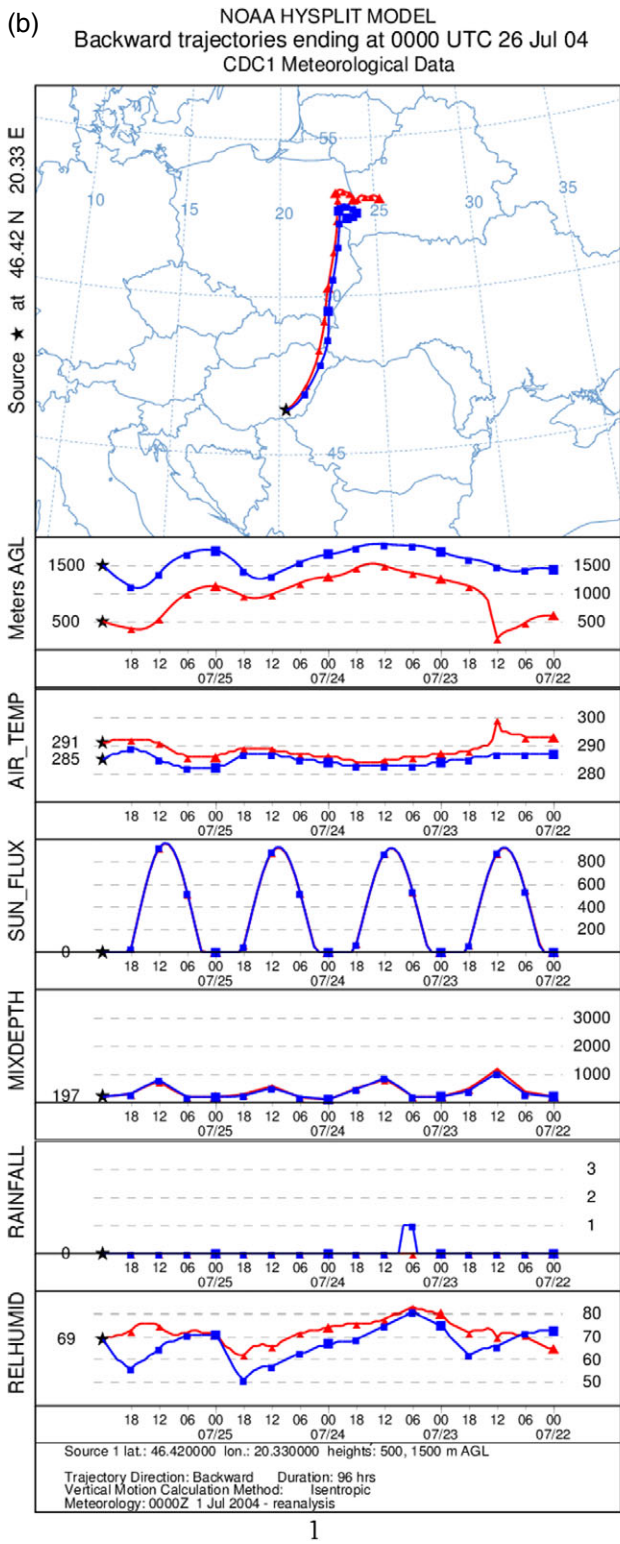


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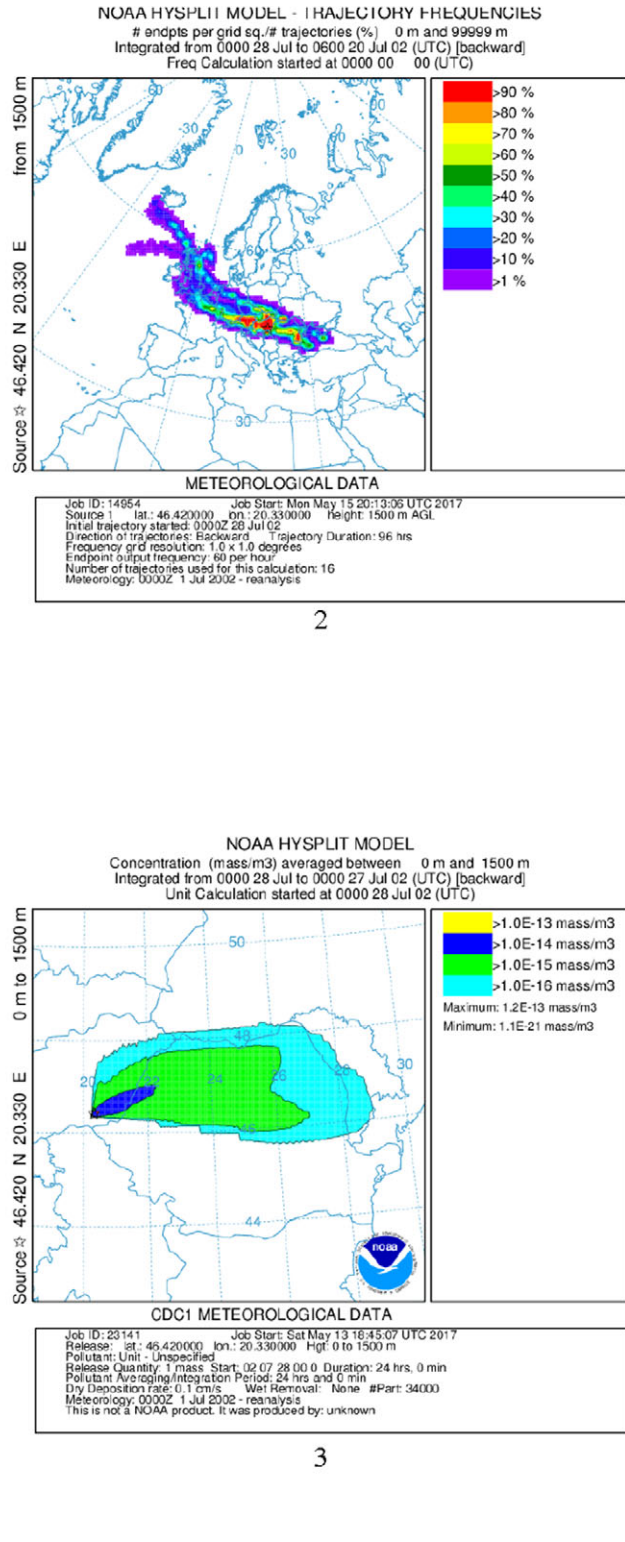
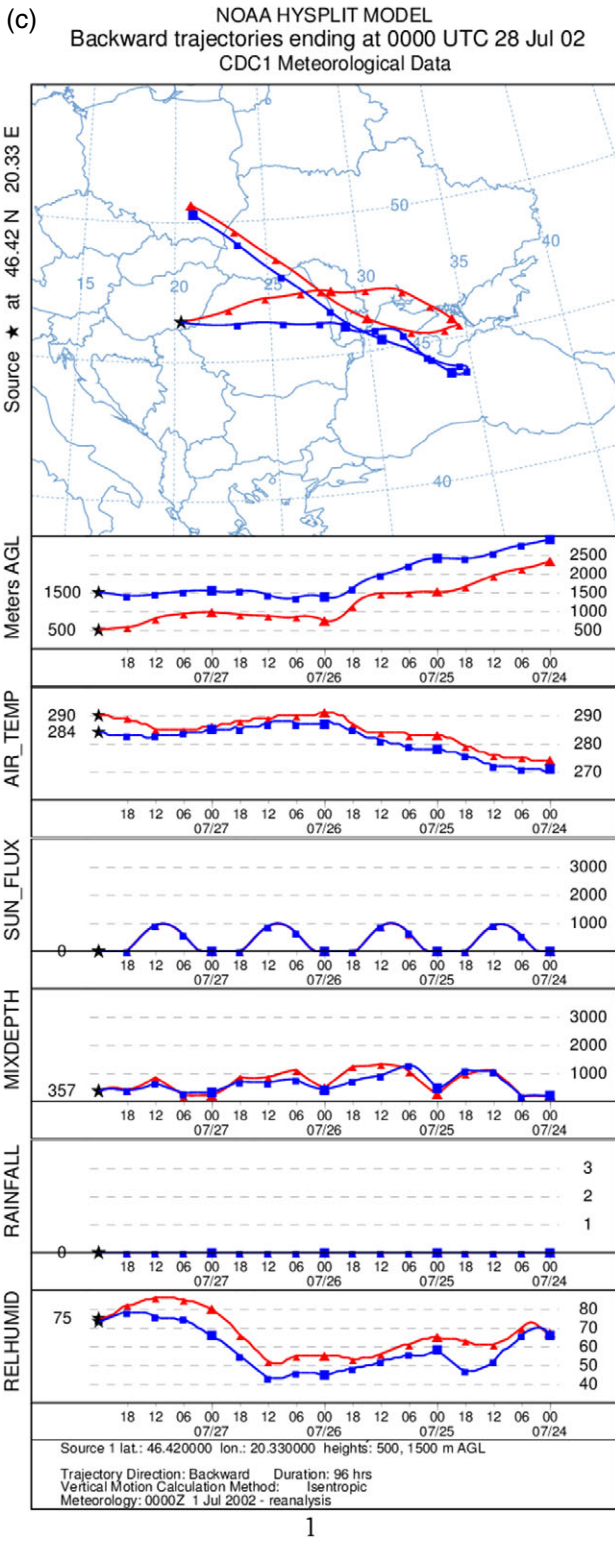


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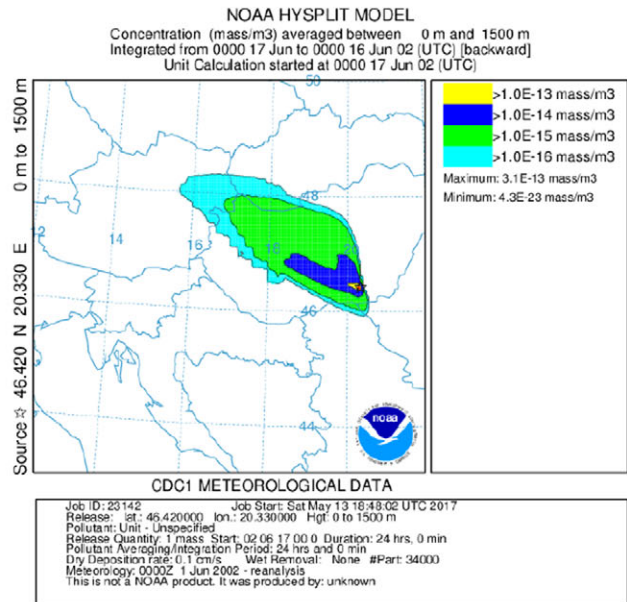
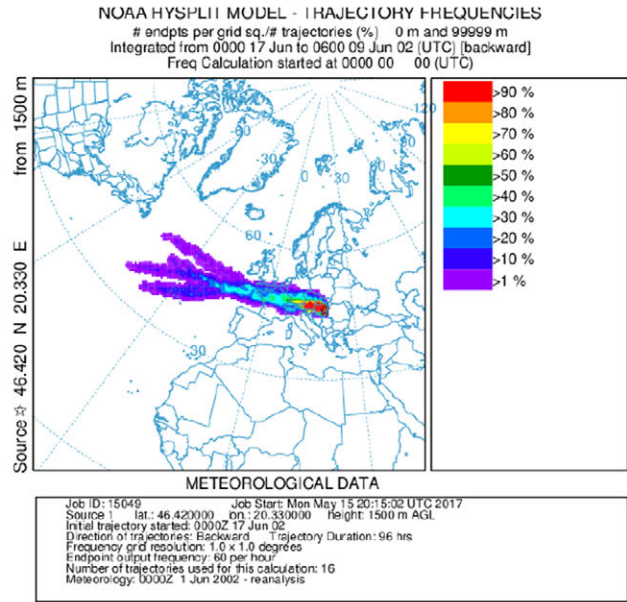
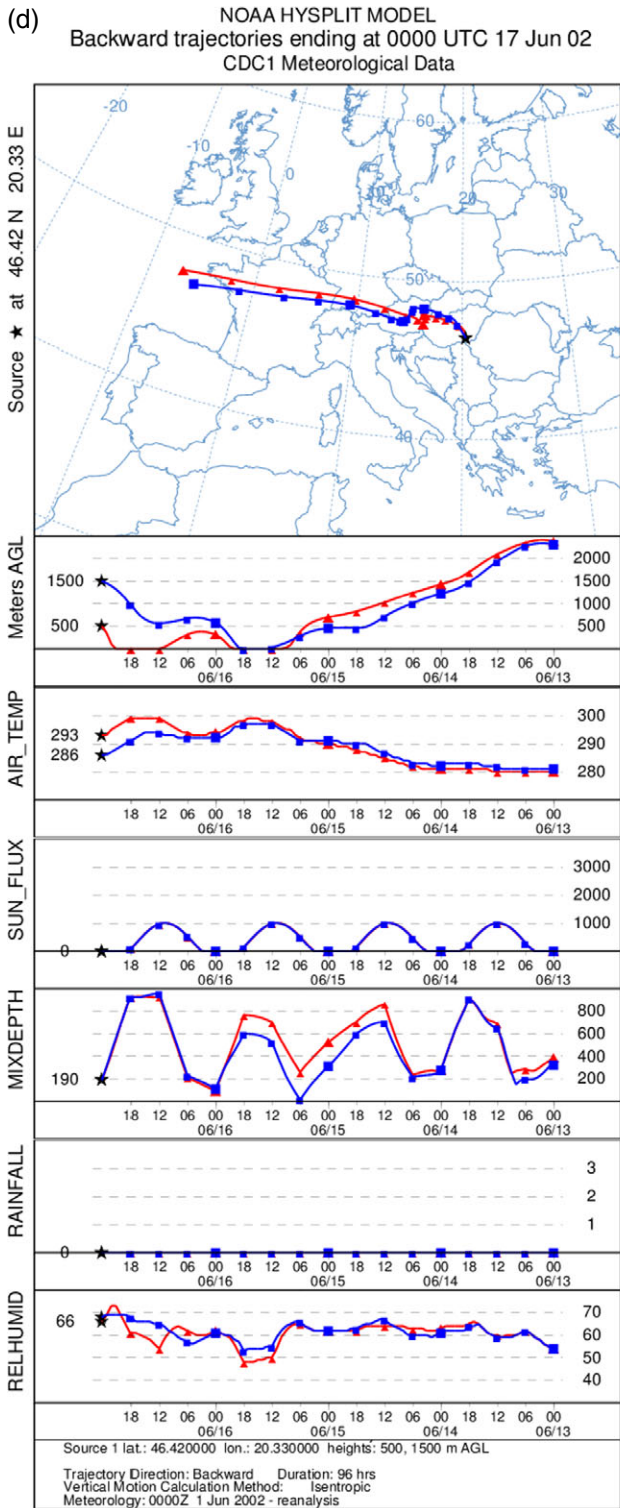


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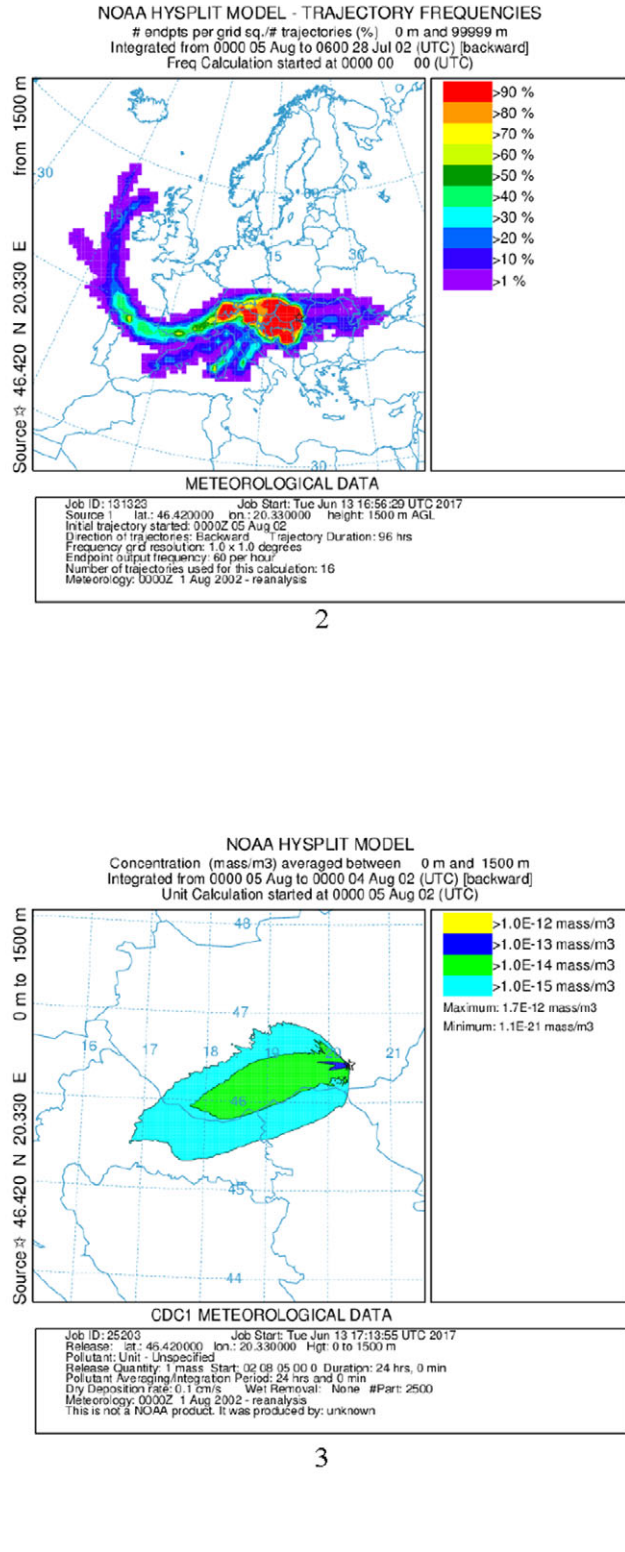
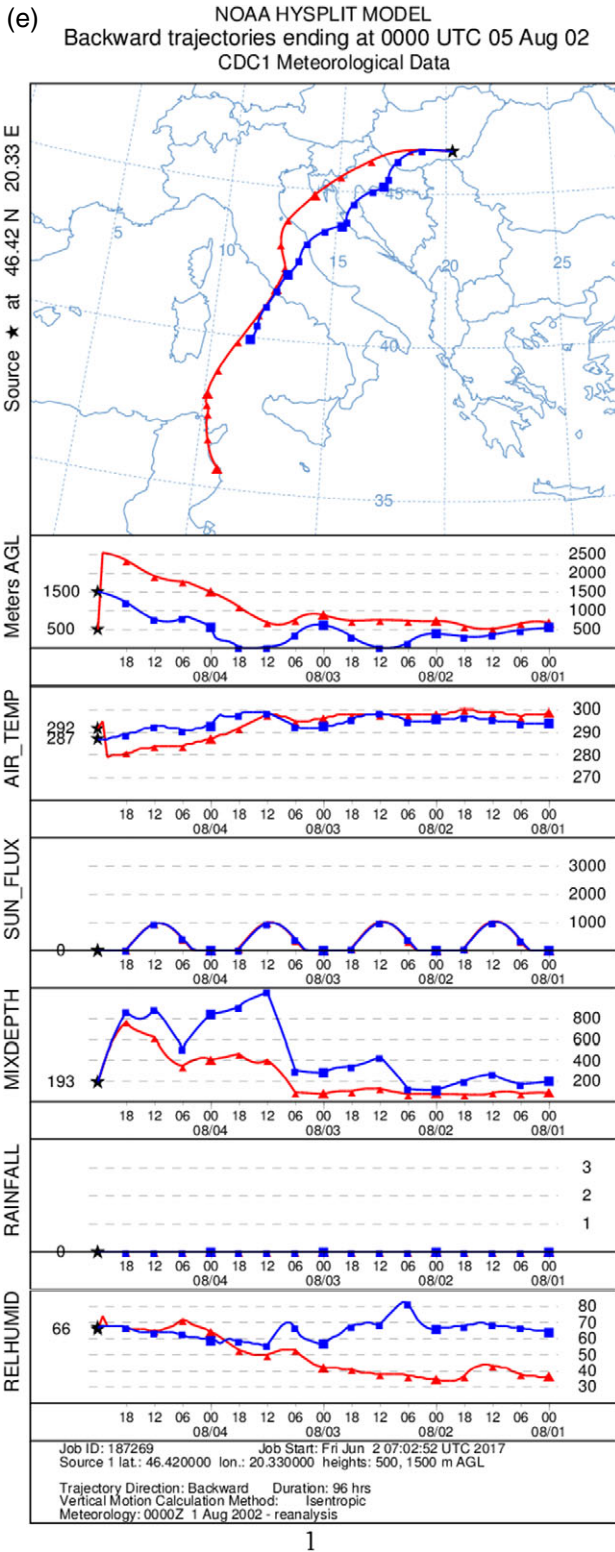


Figure 4 Continued.

occurred rarely (12%), when specimens of this species were caught. *Zurstrassenia figuratus* males and females were caught mostly on days when the back trajectories originated from the west: the Atlantic area (male: 100%, female: 25%) and the Mediterranean (male: 63, female: 46%), respectively. However, some backward trajectories also passed over the Steppic region (male: 13%, female: 25%) or originated from North-Africa (male: 13%, female: 21%) or the Black Sea area (male: 13%, female: 8%) (Fig. 4a–e).

Note that the origin of the back trajectories was analyzed for all 51 flight days in the 3-year (2002–2004) study period. Because an individual back trajectory may have passed through several regions before reaching the target station, the sum of the ratio of the potential source areas may have exceeded 100%.

Meteorological components of the thrips transport

We prepared the maps of 4-day backward trajectories for two arrival heights (500 and 1500 m AGL). Then the height (AGL) of the back trajectories, as well as the ambient air temperature (K), downward solar radiation flux (W/m^2), mixed layer depth (m), rainfall (mm/h) and relative humidity (%) were generated at given heights as a function of time (Fig. 4a1–e1). In addition, we prepared the archive weather charts for the arrival times with the sea level pressure maps, including high and low air pressure areas and weather fronts (Fig. 5a–e), along with archive 850-hPa geopotential (gpdm) and air temperature ($^{\circ}C$) maps for the arrival times (Fig. 6a–e), both for the North-Atlantic–European region. The analysis of the actual meteorological events on the thrips transport was made using the above-mentioned maps.

On 28 June 2004, along the backward trajectories, the air temperature rose above $0^{\circ}C$ only 2 days before the arrival of the back trajectories to the target station (at this time, the height of the 500- and 1500-m back trajectories was approximately 1900 and 2500 m AGL, respectively), when the air parcel was found over Saarland, around the border area between France and Germany. Live specimens, if any, could have got into the air starting from this area and moved on with the prevailing air currents over the target area. The 4-day study period was free of rainfall and

was characterized by undisturbed irradiance. The mixed layer depth never exceeded 1800 m, whereas the relative humidity, with the exception of the middle 2 days, showed near-optimum values for the thrips transport (Fig. 4a1). At the arrival time, a cold front was approaching towards Hungary and characteristic north-west wind could be experienced over the country (Fig. 5a) and $12.1^{\circ}C$ minimum, $33^{\circ}C$ maximum and $22.4^{\circ}C$ mean air temperatures at a nearby station in Szeged (within a distance of 25 km). Furthermore, the height of the 850-hPa geopotential exceeded 150 gpdm over the area of Hungary, with air temperature between 10 and $15^{\circ}C$ (Fig. 6a). Overall, excluding the days 3 and 4, the meteorological conditions were favourable for transporting live specimens to the target area.

On 26 July 2004, the air temperature remained over $7^{\circ}C$ along the whole path of the back trajectories. Despite the balanced course of the air temperature, big changes in the height of the back trajectories indicated disturbances at the beginning and end of their path. Irradiance was weak compared with that on 28 June 2004, and the mixed layer depth hardly reached 1000 m. During the 4-day study period, there was little rain and the relative humidity was in an acceptable range for thrips (Fig. 4b1). At the arrival time, a depression prevailed over Hungary, including the target area and a cold front from north was coming into the country (Fig. 5b), whereas the air temperature parameters at a nearby station Szeged were: a minimum of $19.1^{\circ}C$, a maximum of $33.0^{\circ}C$ and a mean of $24.1^{\circ}C$. The height of the 850-hPa geopotential over Hungary is approximately 1500 m, between 10 and $15^{\circ}C$ but closer to $15^{\circ}C$ air temperatures (Fig. 6b). To sum up, the meteorological conditions were suitable for the long-range transport of thrips. However, the shallow mixed layer, the rain on 23 July and the relatively high humidity (compared with that on 28 June 2004) made the conditions more difficult for them.

As for the 4-day back trajectories for 28 July 2002, a near consistent decrease in the height of the back trajectories is associated with a near consistent increase of air temperature. Excluding the below $0^{\circ}C$ air temperature range at the very beginning on the path of the 1500 m back trajectory, they stayed in a positive temperature range until they reached the target

Figure 4 (a) (1) Arrival of the insects at the target station along selected typical back trajectories, 28 June 2004: *Caliothrips*. Length of the back trajectories arriving at 500 and 1500 m AGL was 2759 and 2931 km, respectively. (2) Trajectory frequencies, integrated from 0000 UTC, 28 June to 0600 UTC, 20 June 2004; trajectory frequency = $100 \times$ number of endpoints per grid square/number of trajectories. (3) Averaged mass concentrations of thrips between 0 m and 1500 m heights AGL, integrated from 0000 UTC, 28 June to 0000 UTC, 27 June 2004. (b) (1) Arrival of the insects at the target station along selected typical back trajectories, 26 July in 2004: *Frankliniella schultzei*. Length of the back trajectories arriving at 500 and 1500 m AGL is 1014 km and 940 km, respectively. (2) Trajectory frequencies, integrated from 0000 UTC, 26 July to 0600 UTC, 18 July 2004; trajectory frequency = $100 \times$ number of endpoints per grid square/number of trajectories. (3) Averaged mass concentrations of thrips between 0 and 1500 m AGL, integrated from 0000 UTC, 26 July to 0000 UTC, 25 July 2004. (c) (1) Arrival of the insects at the target station along selected typical back trajectories, 28 July 2002: *Scolothrips tenuipennis*. Length of the back trajectories arriving at 500 and 1500 m AGL is 2399 and 2511 km, respectively. (2) Trajectory frequencies, integrated from 0000 UTC, 28 July to 0600 UTC, 20 July 2002; trajectory frequency = $100 \times$ number of endpoints per grid square/number of trajectories. (3) Averaged mass concentrations of thrips between 0 and 1500 m AGL, integrated from 0000 UTC, 28 July to 0000 UTC, 27 July 2002. (d) (1) Arrival of the insects at the target station along selected typical back trajectories, 17 June 2002: *Zurstrassenia figuratus*. Length of the back trajectories arriving at 500 and 1500 m AGL is 2259 and 2106 km, respectively. (2) Trajectory frequencies, integrated from 0000 UTC, 17 June to 0600 UTC, 09 June 2002; trajectory frequency = $100 \times$ number of endpoints per grid square/number of trajectories. (3) Averaged mass concentrations of thrips between 0 and 1500 m AGL, integrated from 0000 UTC, 17 June to 0000 UTC, 16 June 2002. (e) (1) Arrival of the insects at the target station along selected typical back trajectories, 5 August 2002: *Zurstrassenia figuratus*. Length of the back trajectories arriving at 500 and 1500 m AGL is 1686 and 1114 km, respectively. (2) Trajectory frequencies, integrated from 0000 UTC, 5 August to 0600 UTC, 28 July 2002; trajectory frequency = $100 \times$ number of endpoints per grid square/number of trajectories. (3) Averaged mass concentrations of thrips between 0 and 1500 m AGL, integrated from 0000 UTC, 5 August to 0000 UTC, 4 August 2002. [Colour figure can be viewed at wileyonlinelibrary.com].

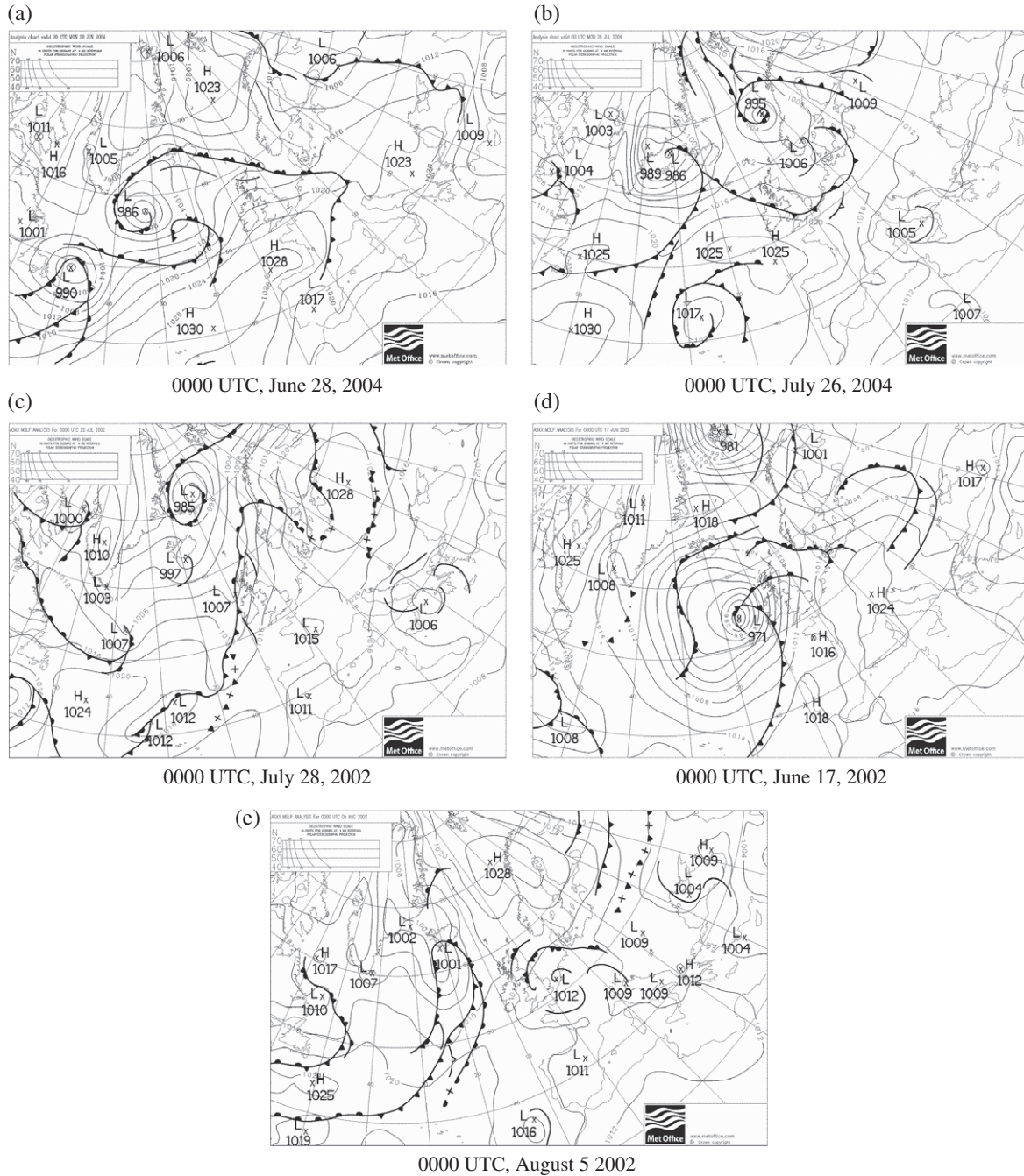


Figure 5 Archive weather charts with sea level pressure maps, including high and low pressure areas and weather fronts for the North-Atlantic–European region (<http://old.wetterzentrale.de/topkarten/tkfaxbraar.htm>) (insect catching day is the day before).

station. The maximum of the irradiance and the mixed layer depth slightly exceeded 1000 W/m^2 and 1200 m , respectively. The period was free of rainfall, and simultaneously the relative humidity was very low (below 50%) and very high (above 80%) on days 3 and 4 (Fig. 4c1), respectively. At the arrival date an occluded front was observed over Hungary (Fig. 5c) with the air temperature parameters from a nearby station Szeged being: a minimum of 18.1°C , a maximum of 31.7°C and a mean of 25.0°C . The 850-hPa geopotential over Hungary lay in the range

152 and 156 gpm , where the air temperature was $10\text{--}12^\circ\text{C}$ (Fig. 6c). Overall, from day 3 before the arrival day, the temperature conditions were suitable, although the mixed layer depth was very low on the arrival day, and the relative humidity was higher than the comfort range for the thrips when they were transported.

Regarding the 4-day back trajectories for 17 June 2002, they steadily descend on the first 2 days, whereas they oscillate within a high altitude range on the last 2 days. The air temperature was

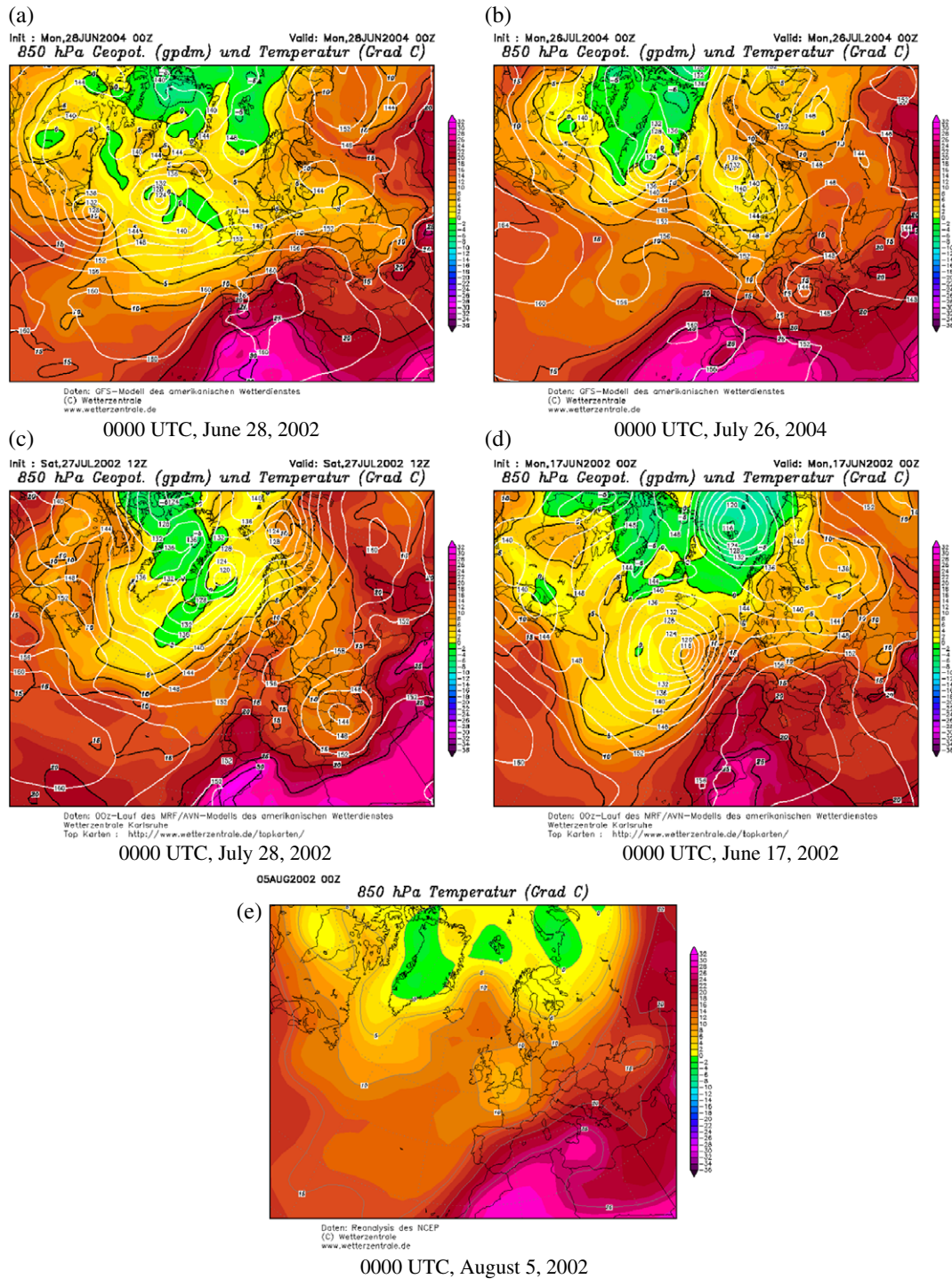


Figure 6 Archive 850-hPa geopotential (gpm) and air temperature (°C) maps for the North-Atlantic–European region (<http://old.wetterzentrale.de/topkarten/fsreaeur.html>) (insect catching day is the day before). [Colour figure can be viewed at wileyonlinelibrary.com].

above 0 °C along the whole path of the backward trajectories. Peak values of the irradiance reached 1000 W/m² every day, whereas the maxima and minima of the mixed layer depth occurred in the afternoon and at dawn, respectively. There was no rain at all during the whole period, whereas the relative humidity was around the optimum in the first 2 days, and it was below

the comfort range in the last 2 days (Fig. 4d1). At the arrival time, a marked high air pressure prevailed in Hungary, weather fronts avoided the area and an intense influx of southern air currents was expected in the forthcoming days (Fig. 5d). The air temperature parameters at a nearby station in Szeged were: a minimum of 18.4 °C, a maximum of 29.0 °C and a mean of

23.7 °C. The height of the 850-hPa geopotential over Hungary was 153–157 gpm, with the air temperature between 12 and 17 °C (Fig. 6d). The above meteorological conditions overall were favourable for the transport of thrips.

Regarding the 4-day back trajectories for 5 August 2002, interestingly, the 500-m back trajectory moved at a higher altitude than the 1500-m equivalent throughout the 4-day period. Moreover, the biggest difference in their height (parallel to their biggest temperature difference) occurred during the last one and half days before their arrival. The air temperature was surprisingly high for the whole path of both back trajectories and fell to 7 °C along the path of the 500-m back trajectory only on the arrival day. Peak values of the irradiance reached 1000 W/m² every day, whereas the maximum height of the mixed layer exceeded 1000 m during the last 2 days before arrival that suggested intense disturbances. There was no rain during the whole period. At the same time the relative humidity was very low during the first 2 days along the path of the 500-m back trajectory. This was what we expected because the back trajectory passed above North-Africa. However, the remaining 2 days before arrival, as well as the whole path of the 1500-m back trajectory, had an optimum range of relative humidity for the insects (Fig. 4e1). According to the weather chart, the study area was front-free, the weather was quiet and strengthening of an anticyclone was expected in the coming days (Fig. 5e). The values of the temperature parameters at a nearby station in Szeged were a minimum of 18.7 °C, a maximum of 29.8 °C and a mean of 23.6 °C. The air temperature on the 850-hPa geopotential over Hungary was 15–16 °C (Fig. 6e).

Based on the above meteorological analysis, except for the days 3 and 4 on 28 June 2004, and despite some less beneficial meteorological parameters on some study days, the environmental conditions were suitable for the transport of thrips along the paths of their 4-day back trajectories.

Concentration and dispersion of the thrips

Maps of averaged mass concentrations (Figs 4a3–e3 and 7a–e) and dispersion (Fig. 8a–e) of thrips between the ground level and the actual height along the path of the 1500-m back trajectory were prepared. The positions (ϕ , λ , h) of the back trajectory, arriving at the target area 1500 m AGL at 0000 UTC, were calculated back in time for every 6 h during the last 24-h period before arrival. In this way, altogether, four back-trajectory coordinates were obtained for which dispersion models were generated. The outputs of the model are figures showing the change in the concentrations of the insects (Fig. 7a–e), as well as other figures showing the degree of deposition (Fig. 8a–e). Altogether, four figures for every 6-h period within the 24-h period, both for concentration and deposition and, in addition, for every 5 study days, $4 \times 2 \times 5 = 40$ maps were generated (Figs 7a–e and 8a–e) (<http://ready.arl.noaa.gov/hypub-bin/disp1.pl>).

The colour scale of the areas from the highest to the smallest concentrations in each figure is: yellow, blue, green and light blue. Coloured areas denote intervals, the values of which can be interpreted as: $1.0E^{-10} = 1.0 \times 10^{-10}$. For example, if the value of the yellow area is $1.0E^{-10}$, whereas that of the blue is $1.0E^{-10}$, this means that at least 10^{-11} th part of the originally released

amount of thrips specimens can be found in the yellow field areas, whereas the blue parts show their concentration between 10^{-10} and 10^{-11} specimens/m³ of ambient air (<http://ready.arl.noaa.gov/hypub-bin/disp1.pl>). [Note that the flow rate of the suction trap is not available. Therefore, we cannot determine the most interpretable unit of the real concentration (number of insects in unit volume of air). Instead, we calculated a theoretical concentration.]

Concentration maps. The change in concentration (i.e. the change in the number of thrips specimens) is presented in association with the study days, for each occasion, calculating (i) backward, going 24 h back in time before the arrival date (Fig. 4a3–e3) and (ii) forward, starting with 24 h preceding the arrival date and calculating the concentration for every 6 h during the last 24-h period (Fig. 7a–e). The results are in accordance with the back-trajectory analysis (Fig. 4a1–e1), namely both the 24-h backward plumes (Fig. 4a3–e3) and the 6-hourly forward concentration plumes (Fig. 7a–e) follow quite well the back trajectories in each case. Regarding the averaged mass concentration of thrips, the light blue part (i.e. 10^{-15} th part for Fig. 4a3, and Fig. 4e3, as well as 10^{-16} th part for Figs. 4b3–4d3, respectively) of the concentration plume can be detected in 1 m⁻³ of air over the area 24 h before arrival. Then, after 24 h, we can find 1×10^{-10} (Fig. 4a3,e3) and 1×10^{-11} (Fig. 4b3–d3) specimens in 1 m³ of ambient air in the target area, respectively. At the same time, the 6-h concentration plumes nearest the target area (1800–2400) only reached Hódmezővásárhely (46.42 N; 20.33 E) on one of the five study days, namely on 26 July 2004 at 0000 (Fig. 7b4). The modelled concentration can be interpreted as follows. Six hours after the emission, 10^{-14} th part of the emission could be detected in 1 m⁻³ of air in the target area. Namely, if a unit amount of thrips specimens/m³ of ambient air had taken off for flight, then, after 6 h, it would have found 1×10^{-11} specimens in 1 m³ of ambient air in the target area (Fig. 7b4).

Deposition maps. The deposition of the thrips specimens is also shown on the study days and, similar to the concentration maps, it is calculated backwards in time for every 6 h during the last 24-h period (Fig. 8a–e). The resulting deposition trails (Fig. 8a–e) followed best the back trajectories arriving in the target area at 0000 on 26 July 2004 (Figs 4b1 and 8b), 28 July 2002 (Figs 4c1 and 8c) and 17 June 2002 (Figs 4d1 and 8d). The 6-h deposition curves nearest to the target area (1800–2400) practically reached Hódmezővásárhely (46.42N; 20.33E) only at 0000 on 17 June in 2002 (Fig. 8b4). The modelled deposition can be interpreted as follows. Six hours after the emission, 10^{-12} th part of the emission deposited in the target area. In other words, if a unit amount of thrips specimens/m³ of ambient air had taken off for flight, then, after 6 h, 1×10^{-9} specimens would have been deposited in Hódmezővásárhely (Fig. 8b4). As a result, the deposition of thrips specimens compared with their concentration was two orders of magnitude higher (Figs 7b4 and 8b4). Note that, on 26 July 2004 (Fig. 4b1) and 28 July 2002 (Fig. 4c1), dispersion is restricted to a long and substantially narrow area; hence, it is much more concentrated compared with that on the other two study days (Fig. 8a–e).

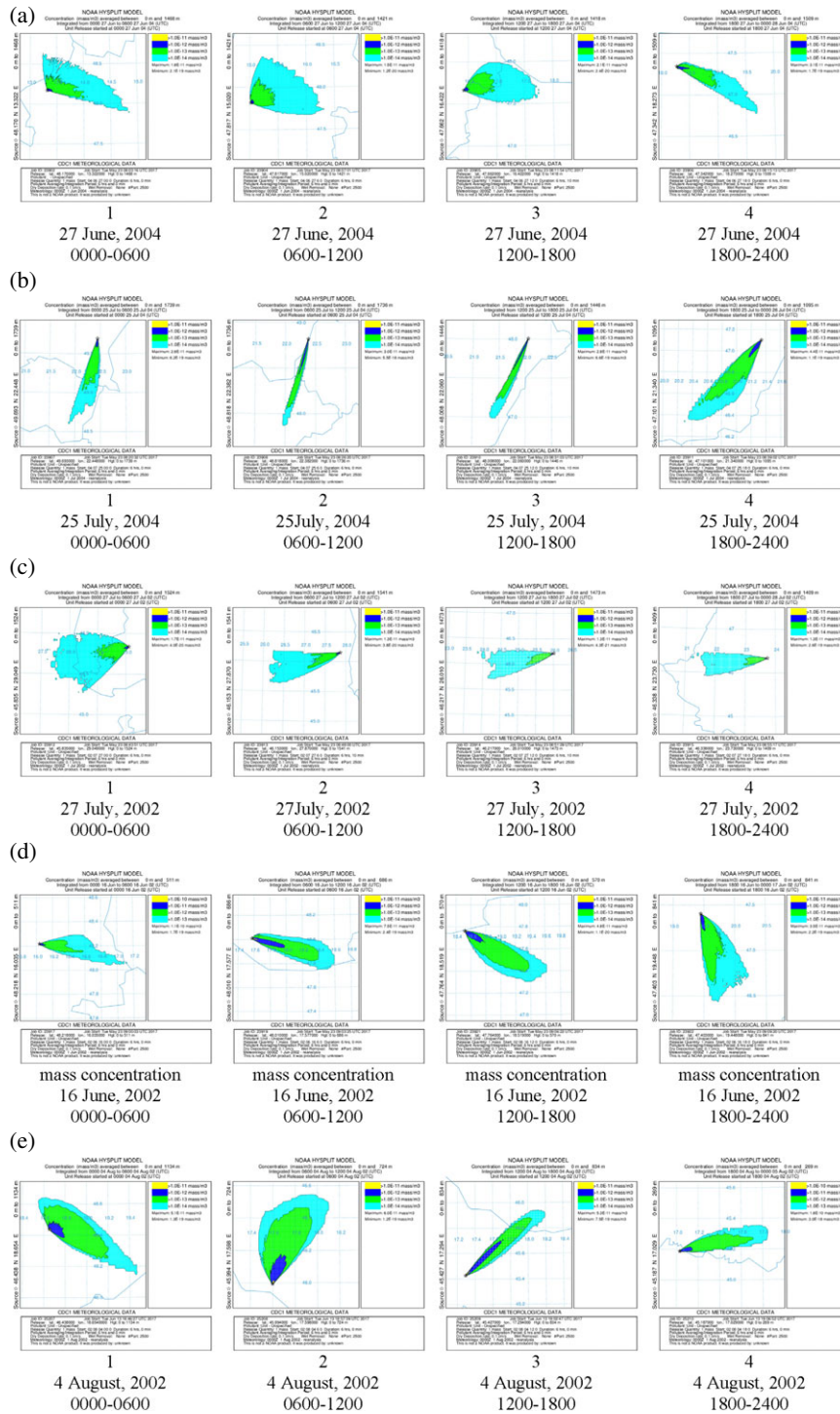


Figure 7 (a) Concentration averaged between the ground level and the actual height along the path of the back trajectory arriving at the target area at 1500 m AGL at 0000 UTC, calculated backwards in time for every 6 h during the last 24-h period before its arrival (mass/m³), 27 June 2004. (b) Concentration averaged between the ground level and the actual height along the path of the back trajectory arriving at the target area at 1500 m AGL at 0000 UTC, calculated backwards in time for every 6 h during the last 24-h period before its arrival (mass-m⁻³), 25 July 2004. (c) Concentration averaged between the ground level and the actual height along the path of the back trajectory arriving at the target area at 1500 m AGL at 0000 UTC, calculated backwards in time for every 6 h during the last 24-h period before its arrival (mass/m³), 27 July 2002. (d) Concentration averaged between the ground level and the actual height along the path of the back trajectory arriving at the target area at 1500 m AGL at 0000 UTC, calculated backwards in time for every 6 h during the last 24-h period before its arrival (mass/m³), 16 June 2002. (e) Concentration averaged between the ground level and the actual height along the path of the back trajectory arriving at the target area at 1500 m AGL at 0000 UTC, calculated backwards in time for every 6 h during the last 24-h period before its arrival (mass/m³), 4 August 2002. [Colour figure can be viewed at wileyonlinelibrary.com].

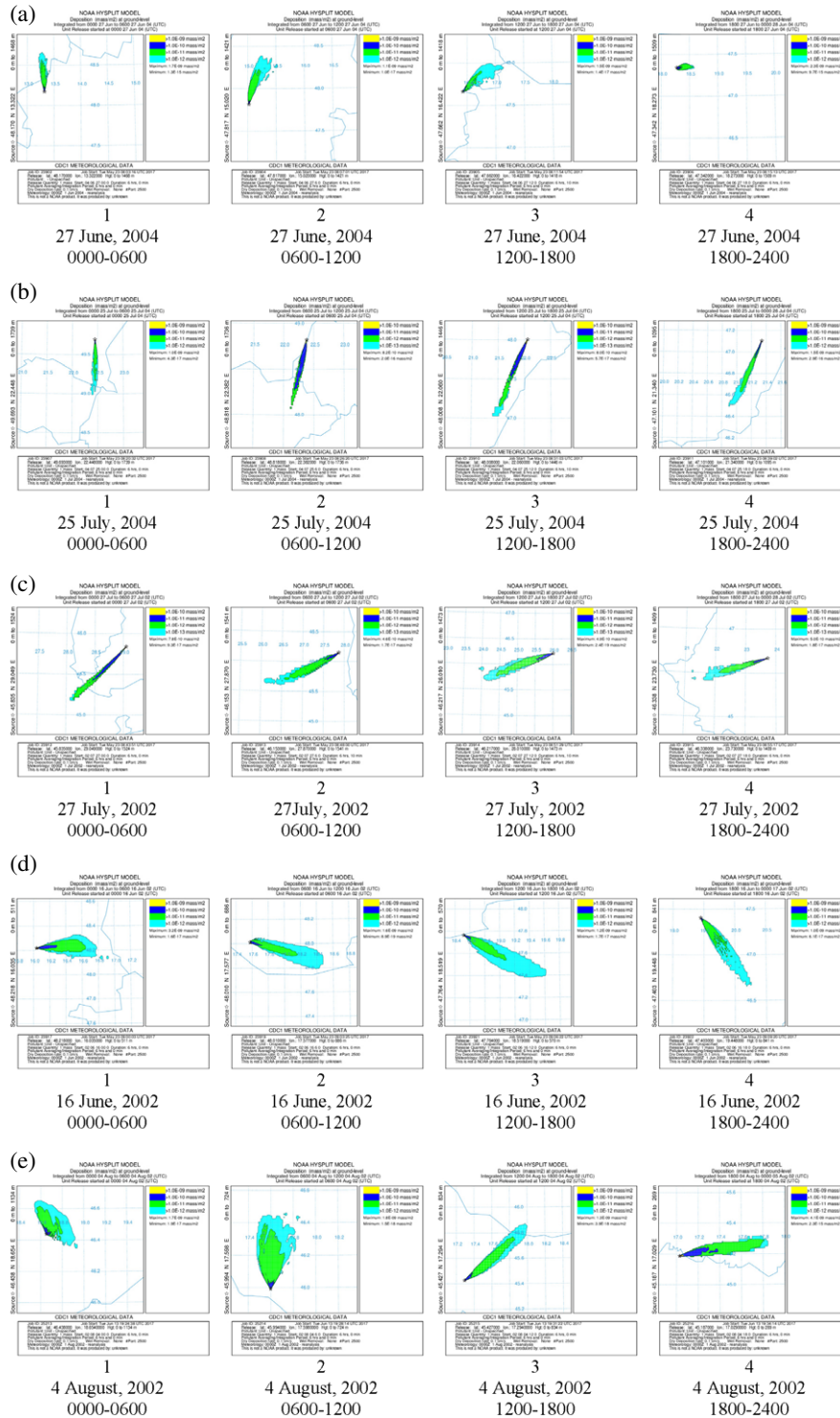


Figure 8 (a) Deposition at ground level along the path of the back trajectory arriving at the target area at 1500 m AGL at 0000 UTC, calculated backwards in time for every 6 h during the last 24-h period before its arrival (mass/m²), 27 June 2004. (b) Deposition at ground level along the path of the back trajectory arriving at the target area at 1500 m AGL at 0000 UTC, calculated backwards in time for every 6 h during the last 24-h period before its arrival (mass/m²), 25 July 2004. (c) Deposition at ground level along the path of the back trajectory arriving at the target area at 1500 m AGL at 0000 UTC, calculated backwards in time for every 6 h during the last 24-h period before its arrival (mass/m²), 27 July 2002. (d) Deposition at ground level along the path of the back trajectory arriving at the target area at 1500 m AGL at 0000 UTC, calculated backwards in time for every 6 h during the last 24-h period before its arrival (mass/m²), 16 June 2002. (e) Deposition at ground level along the path of the back trajectory arriving at the target area at 1500 m AGL at 0000 UTC, calculated backwards in time for every 6 h during the last 24-h period before its arrival (mass/m²), 4 August 2002. [Colour figure can be viewed at wileyonlinelibrary.com].

Discussion

We prepared the maps of 4-day backward trajectories for two arrival heights (500 m and 1500 m AGL). Then we generated and mapped the height (AGL) of the 4-day back trajectories, as well as the values of the ambient air temperature (K), downward solar radiation flux (W/m^2), mixed layer depth (m), rainfall (mm/h) and relative humidity (%) at every 6-h period as a function of time (Fig. 4a1–e1). The maps were represented using the default projection offered by the HYSPLIT READY website (<http://www.arl.noaa.gov/ready/hysplit4.html>) (Fig. 4a–e). In addition, we prepared archive weather charts for the arrival dates with the sea level air pressure maps, including high and low air pressure areas and weather fronts (<http://old.wetterzentrale.de/topkarten/tkfaxbraar.htm>) (Fig. 5), along with archive 850-hPa geopotential (gpm) and ambient air temperature ($^{\circ}C$) maps for the arrival dates (Fig. 6), both for the North-Atlantic–European region (<http://old.wetterzentrale.de/topkarten/fsreaeur.html>) (Fig. 6), were also represented (Draxler *et al.*, 2016). The discussion of the actual meteorological events on the thrips transport was based on the above-mentioned maps. To detect any uncertainty in the paths of the back trajectories, a trajectory frequency analysis was made for all the four study days (Fig. 4a2–e2). Moreover, maps of backward and forward concentrations, as well as those of forward deposition were generated using the HYSPLIT READY website (<http://www.arl.noaa.gov/ready/hysplit4.html>).

Back-trajectory analysis

The results of the back-trajectory analysis showed that, somewhat surprisingly, on the study days, only a small percentage of the backward trajectories arrived in the target area from Africa. The results suggest that the captured thrips species could survive long distance transport at low-level trajectories and establish new populations in a distant geographical area (i.e. in several parts of Europe). The 4-day backward trajectories presume that thrips may arrive in the target area by long-range transport from Western Europe, the eastern part of Europe and north of Europe.

It is known that three of the captured species are native in subtropics (zur Strassen, 1965, 1968; Vierbergen & Mantel, 1991). *Zurstrassenia figuratus* is native in the Canary Islands and Morocco. This species frequently occurs on the seashore. It was described by zur Strassen from Cercle de Goulimine, Ait-Hassine, Morocco from flowering *Limonium sinuatum* (zur Strassen, 1968). *Scolothrips tenuipennis* was originally described based on a single male acquired in the Canary Islands (Gran Canaria, Hierro; zur Strassen, 1983, 2003). *Scolothrips tenuipennis* was described originally from a male specimen taken in the Canary Islands, Gran Canaria, Barranco de Mogán (zur Strassen, 1965) and the female specimen was found later in the same islands in Hierro (zur Strassen, 1983). Later, the species was recorded in Cape Verde Islands (zur Strassen, 1993, 2003). The female specimen of *S. tenuipennis* was also found in Iran (Minaei & Abdollahi, 2015). *Caliothrips* species known from North-Africa are pests of the faba bean (Remane, 1961) and cotton (Bagnall & Cameron, 1932; Ananthakrishnan, 1993). *Frankliniella schultzei* (Trybom) is distributed in North and

South America, Africa and Australia, and in the Oriental region (Mound, 1997), as well as in Israel, Egypt, Spain, Canary Islands and Morocco, and it was introduced in the temperate region of Europe (Netherlands, Denmark, England) in greenhouses several times (zur Strassen, 2003). *Frankliniella schultzei* is a key pest in tomato and cucumber fields in South America and in Florida (Monteiro *et al.*, 2001; Jones, 2005; Kakkar *et al.*, 2012). In Europe, it was observed only in greenhouses with tropical conditions in Denmark, Netherlands and England. It is a polyphagous pest that feeds on various cultivated plants (Vierbergen & Mantel, 1991), ornamental and vegetable hosts in different parts of the world (Milne *et al.*, 1996). The major hosts of *F. schultzei* are cotton, groundnut, beans and pigeon pea. However, as a result of its polyphagous feeding behaviour, *F. schultzei* also attacks tomatoes, sweet potatoes, coffee, sorghum, chillies, onions and sunflowers (Hill, 1983). *Frankliniella schultzei* can cause both direct and indirect damage to crop. Both adults and nymphs feed on pollen and floral tissue, leading to flower abortion. Severe infestations can cause discoloration and stunted growth of the plant. However, indirect damage by *F. schultzei* is the result of viral transmission (Amin and Palmer, 1985). This thrips species is one of the important vectors of TSWV (Tomato Spotted Wilt Virus) (Vierbergen & Mantel, 1991; Wijkamp *et al.*, 1995; Riley *et al.*, 2011).

We should add that European greenhouse populations can and are controlled probably if pest status is clear. A huge passive transport by human transportation systems remains an open question, especially if a species cause no easy to see threat.

Uncertainty of the single back trajectories

To obtain reliable information on the path of the back trajectories, a trajectory frequency analysis was performed for the five study days. We found that, in certain cases, the single backward trajectories accurately reflect the trajectory frequencies (Fig. 4a2,d2), whereas, in other cases, there is only a loose relationship between them (Fig. 4b2,c2,e2).

Note that trajectory error is caused by a physical and a numerical component. Absolute trajectory error (km) is typically 15–30% of the travel distance (Stohl, 1998). The physical component of the error is related to how well the numerical fields estimate the true flow field. There is no way of knowing this without independent verification data, whereas the numerical component of the error can be estimated. This error arises from the integration error (part of which is a result of truncation) and an error as a result of the data resolution: trying to represent a continuous function, the atmospheric flow field, with gridded data points of limited resolution in space and time. The integration error can be estimated by computing a backward trajectory from the forward-trajectory endpoint: the error is then half the distance of the final endpoint and starting point. The resolution error can be estimated by starting several trajectories about the initial point (offset in the horizontal and vertical). The divergence of these trajectories will give an estimate of the uncertainty as a result of divergence in the flow field (R. Draxler, personal communication).

Scale affect of convective plumes to air and insect motions

A given resolution of a system of atmospheric motions may play a unique role in the dispersal of a given bio-aerosol, although it may be not significant in the dispersal of other bio-aerosols.

Recent advances in meteorological technologies and techniques provide new insights into micro-, mezo- and macroscale aerobiological processes. Namely, Lidar systems (Behrendt, 2005) may identify microscale characteristics of atmospheric turbulence over agricultural fields that cannot be clearly determined by conventional site-specific atmospheric sensors. Also, super-pressure balloons may be tracked several hundred kilometres per day that follow atmospheric pathways of migrating insects between agricultural regions (Westbrook & Isard, 1999). Such atmospheric trajectories often reveal a substantial day-to-day variation of aerobiological pathways and, consequently, affect for example the risk of pest infestations. Furthermore, Doppler weather radar (Bringi & Chandrasekar, 2001) can measure the aerial abundance, speed and displacement direction of concentrated bio-aerosol over areas larger than 1000 km².

Atmospheric motion systems are generally positively correlated in space and time scales. In other words, motions that occur in small volumes of air have short life spans and motions involving extensive volumes have substantially longer time spans. They can range from wind blowing across a rough surface generating tiny eddies that persist for a few seconds, to the largest scales, such as the westerlies, that span the globe and continue for a long time. Hence, the atmospheric motion systems in which bio-aerosol disperse may require substantially different measurement protocols (Westbrook & Isard, 1999).

Passive transport or active migration, or both?

Insects, as small organisms are a kind of bio-aerosol that have an independent ability to move. In this sense, migration is the proper term for expressing their airborne locomotion. At the same time, in general, their locomotion always has two components: (i) their self-movement (i.e. migration) and (ii) their displacement by the winds (i.e. transport, dispersal or dispersion). In other words, both 'transport' and 'dispersal' and 'dispersion' denote a pure passive displacement of the insects. However, although most often both components influence the movement of insects, it may happen that they are transported without the migratory (i.e. self-movement component). Namely, under the formation of a developed and extensive atmospheric instability and, hence, strong updrafts, they may rise to high altitudes, where low air temperatures substantially decrease their self-movement ability, and air temperature may even fall below 0 °C and they freeze. From this moment on, because of the lack of the ability of self-movement (including wingless thrips), we refer only and exclusively to their transport. Note that this condition may be fulfilled even below sufficiently low positive air temperatures.

Regarding the terms 'transport', 'dispersal' or 'dispersion', as another component besides the migratory component, we prefer the term 'transport' because only this one suggests a definite direction; in addition, the meaning of this term is independent of that of the other two terms. Note that atmospheric transport ensures that the insects can fly at a speed much greater than their own flying speed. They can be carried by the wind.

In addition, there is another mode of the transportation of thrips. Namely, when international imports of plants, thrips are frequently intercepted. Thus major international trade centres (e.g. large harbours in the Netherlands) are other likely routes of entry for spreading thrips (Vierbergen, 1995).

Migratory behaviour and flight related meteorological conditions for Thysanoptera species

Regarding flight height, flight speed and flight distance, as well as flight activity, flight time and flight-related weather elements, the international literature contains relatively little information on thrips.

Thrips are very small insects. The length of the adult species varies from between 0.8 and 1.6 mm (Gillott, 2005). Besides pollen grains and spores, they are subjects of aerobiological research (Lewis, 1973; McManus, 1979). Apart from active flight, thrips, even wingless ones, can also be picked up by strong updrafts and transported long distances. As an example, there is a record of a specimen caught in the Yellow Sea 460 km from the nearest land, at wind speeds of 28–32 km/h (Lewis, 1973). In addition, wind-aided dispersal of thrips species has been found over 1600 km of sea between Australia and South Island of New Zealand (Mound, 2003). Using aircraft trapping, Glick (1939) collected Thysanoptera (winged adult specimens) in the upper atmosphere as high as 11 000 ft (approximately 3000 m), although most were taken at altitudes less than 1000 ft (approximately 300 m). As a comparison, Westbrook (2008) found that moth migration occurs at elevations of up to 2350 m. Cheng and Sun (2016) filmed the take-off flight of thrips using a high-speed camera. They established that the thrips, which have bristled wings, flew at a much smaller wing-tip speed (0.68 m/s) than flies (2.5 m/s).

Apparently, noxious (e.g. *F. schultzei*) (Hoddle *et al.*, 2012) species have the possibility to establish populations in new regions of Europe for a longer period, if favourable conditions are provided by the current climate change. For example, the warming climate is favourable for the spread of bio-aerosols, such as spores (Werner, 2004) and pollen (Makra *et al.*, 2016) in Europe by long-distance transport. Moreover, dangerous human and animal pathogenic insects (vectors) may also occur in Hungary as a result of climate change (Trájer *et al.*, 2013, 2015). The warming climate, with milder winters and increasingly warmer summers, provides more favourable circumstances for the Thysanoptera species to be transported passively over long distances in Hungary and the neighbouring countries as well (Stange & Ayres, 2010; Bebbler *et al.*, 2013; Björkman & Niemelä, 2015). It is important to consider the possibility of long-range transport of other noxious insects (e.g. vectors of human diseases too).

Most medium-size or larger winged insects can control the duration of their flight. Most species fly in sunny, calm weather with slight convection. Thrips are day-flying insects and generally stop flying just before sunset. However, it should be noted that nocturnal migration of insects can also be important. Thrips often become trapped above temperature inversions, and are dispersed day and night until convection erodes the inversions, allowing these insects to descend to the surface (Drake, 1985; Wolf *et al.*, 1986). The mass flight of thrips is closely

associated with air temperature exceeding a common threshold zone of 19 and 21 °C (Lewis, 1964). The frequency curve of the mean daily flight numbers displays a midday–early afternoon peak. Furthermore, the mean daily flight period is species dependent, amounting to 10–12 h a day (Lewis & Taylor, 1964; Lewis, 1973; Orosz *et al.*, 2016; WMO and FAO, 2016). However, according to Lewis (1973), thrips may remain airborne and travel in the wind for approximately 16 h. Regarding the mean wing-tip speed (0.68 m/s) and mean daily flight time (10–12 h) of thrips, they can travel on average around 60 km per day and exclusively by their self-movement (i.e. migration) (note that the additional effect of wind-related transport has not been taken into account here). The above findings confirm our results, according to which viable thrips can travel several thousand kilometers from the source area to the target station.

There is no direct evidence indicating that the examined species arrived at the target area passively (i.e. via long-distance transport by air currents) or by active flight.

According to McManus (1979), the airborne number of the individuals of any insect species that can be trapped at any location, altitude or time depends on many variables. These include the size and species composition of the source area, the seasonal and diurnal variation in the number of thrips, the behaviour of the dispersant population, and the meteorological factors prior to and during the collection. Air temperature (by flight activity threshold of insects and their passive ‘lift-up’ by thermal convection), furthermore, surface and upper winds are important factors in the initiation of airborne dispersion.

During warm and humid weather, adults may climb to the tips of plants to leap and catch air currents (Mound, 2003). In a case study, Orosz *et al.* (2016) analyzed the dependence of the mass flight of thrips on weather elements. They found that sunny hours with undisturbed irradiance are proportional to the migration of *Haplothrips angusticornis* (Thysanoptera: Phlaeothripidae). At the same time, the role of air pressure is not clear. The number of migrating specimens definitely decreased between air pressure levels in the range 1000–1008 hPa and then started to increase again.

The threshold air temperature for the take-off of Thysanoptera is usually 17–20 °C in the temperate regions (Taylor, 1963). However, Orosz *et al.* (2016) found that the minimum air temperature for the flight activity of adult *Haplothrips angusticornis* (Thysanoptera: Phlaeothripidae) was 5 °C, whereas the maximum air temperature was 35 °C. In addition, the insects in flight were most active at 23 °C average air temperature. The optimum air temperature conditions for the mass flight of *H. angusticornis* are: 19 °C, minimum temperature; 29 °C, maximum temperature; and 23 °C, mean temperature (Orosz *et al.*, 2016). As a comparison, the minimum air temperature for lift-off and the active flight of moths is 15 °C, whereas the maximum air temperature for lift-off is 29.5 °C (Sturtevant *et al.*, 2013). For the male fly, an air temperature of around 10 °C prevents flight (Pagabeleguem *et al.*, 2015). The thermal threshold for the flight activity of the adult seed wasp is around 16 °C (Lander *et al.*, 2014). This agrees with values recorded for the bean aphid (13–15 °C; McManus, 1979) and three Homoptera species (14 °C; Wellington, 1945a). Carlson *et al.* (1992) consider as important the sufficiently high air temperatures for flight and the lack of major precipitation along all but the terminal portions of the back trajectories. In this

way, the arrival points of the 500- and 1500-m back-trajectory heights meet the air temperature requirement favourable for the flight of insects (10.0–29.5 °C) on all trapping days. At the same time, (i) when the arrival date was 0000 UTC, 28 June 2004, both the 500- and 1500-m back trajectories reached the height of approximately 1500 m AGL 36 h before arrival. During this period, the air temperature (flight minimum temperature: 5 °C; Orosz *et al.*, 2016) along the back trajectories made the independent flight possible (i.e. the migration of thrips). (ii) This was also the case for the arrival date 0000 UTC, 28 July 2002, when the 500-m (1500-m) back trajectory exceeded the flight minimum temperature at a height of 1600 m (2400 m) AGL, 90 h (84 h) before arrival. Regarding rainfall, only one occasion can be noted: 66–63 h before the arrival date (0000 UTC, 26 July 2004), 1 mm rainfall was recorded. Therefore, according to the rainfall and air temperature data, Thysanoptera species could be transported from the Atlantic biogeographical region to the target area via long-distance air currents either (i) passively and/or (ii) actively if the ambient air temperature exceeded the flight minimum temperature all along their way.

For a better understanding, information on precipitation must also be taken into consideration. Note that there is little information on rainfall thresholds of the migration of insects, including thrips. As an example, the findings of Sturtevant *et al.* (2013) could be mentioned here, according to which moths do not take off during ‘heavy rain’ ($P_{\max} = 2.5$ mm). (After sunset, if the surroundings are wet and the air humidity is high, taking off may be difficult for moths.) From the 22 flight days examined, rainfall at the target station exceeded the 2.5 mm threshold on 2 days, namely 24.8 mm on 17 June 2002 and 2.7 mm on 12 August 2002. These findings suggest that heavy rainfall at the target station may not prevent the capture of insects. Note that another classification of rain intensity is also available. For synoptic purposes, rain showers are classified as ‘slight’, ‘moderate’, ‘heavy’ or ‘violent’ for rates of accumulation of about 0–2, 2–10, 10–50 or > 50 mm/h, respectively (U.K. MetOffice, 2007). It should be added that high relative humidity in general, and especially in the evening (adverse air temperature–relative humidity relationship; i.e. decreasing air temperature increases relative humidity and vice versa) makes flying difficult for thrips. Nevertheless, we should note that (i) the above definitions of ‘heavy rain’ [daily amount (U.K. MetOffice, 2007) versus within-day intensity (Sturtevant *et al.*, 2013)] cannot be compared and (ii) other components also should be taken into account here (e.g. the duration of rainfall, with this parameter being related to intensity, and what time of the day the rain falls, as well as the strength of irradiance and wind).

The optimum level of the relative humidity for the mass flight of thrips was found to be approximately 62%. These parameters display an inverse relationship; namely, higher levels of relative humidity involve reduced mass flight and migration and vice versa (Orosz *et al.*, 2016). Although thrips have water resistant bodies (Ortega-Jiménez *et al.*, 2016), in the case of higher than optimum relative humidity (in general in the evening and at night), their wings take on moisture and hence become heavier. This makes their flight more difficult, and this is why they fly with difficulty or do not fly at all during periods of high relative humidity.

It should be noted that, during transportation at high altitudes, there are unfavourable conditions (low air temperature) for small insects such as the thrips species. Early experiments showed that air temperature is the limiting factor in determining whether an insect could attain or survive high-altitude dispersion (Wellington, 1945a,b). According to Wellington (1945b), dispersion is obviously a very hazardous process for insects; the probability of survival for those species that are passively blown by wind is low. At a height of 3–4.5 km (under summer conditions in temperate North America), air temperatures are around 0 °C. Small insects (aphids) can withstand these low air temperatures for only a short time and therefore would probably die at higher altitudes. However, at lower altitudes (between 305 and 1219 m), 99% of the trapped insects (mostly aphids) were alive and capable of reproduction (Taylor, 1960). The height of 71.1% of our trajectories was below 1500 m (whereas 62.5% of the North-African trajectories were also below 1500 m). In this calculation, all 104 back trajectories (arrival heights of 500 and 1500 m AGL, respectively) on the 51 insect catching days were checked using the altitude graphs of the HYSPLIT model and the back trajectories that passed below an altitude of 1500 m were taken into account.

In total, based on the back-trajectory analysis (Fig. 4a–e), archive weather charts with sea level pressure maps (Fig. 5) and archive 850-hPa geopotential and air temperature maps (Fig. 6), strong currents of long-range migrations can be related to cyclones (especially to the fore part of their air flow system) and/or disturbances. Low-level jet streams associated with weather fronts may also be important in providing transport of thrips.

Insects versus vertical air motions

Besides information on meteorological and ecological parameters, the convective state of the atmosphere plays an important role in the long-range transport of insects.

Rainey (1963) reported a finding on the long-range progressive displacement of Desert Locust swarms, over distances ranging from 600 to 3500 km within periods ranging from 5 days to 2 months and found that the distribution of Desert Locust on scales from a hundred to thousands of kilometers is not merely correlated with but is to a very large extent determined by the corresponding low-level wind fields.

Locust swarms move under the influence of large-scale weather patterns on a synoptic scale. Namely, cool and overcast weather (having a cyclonic character) favours stratiform (locusts spread out horizontally in the atmosphere) swarms, whereas, during clear sky and undisturbed irradiance (anticyclonic character), convective updrafts promote cumuliform (locusts spread out vertically in the atmosphere) swarms. A locust swarm is usually displaced at slightly less than the wind speed and may easily move 100 km or more in a day. In the absence of any wind, locusts fly at approximately 3–4 m/s. It is not clear with cumuliform swarms which wind level determines displacement. Stratiform swarms fly low up to heights of 100 m; in contrast, cumuliform swarms fly up to heights of 1000 m or more. Individuals have been detected by radar up to heights of 1800 m. Swarms start to settle approximately 1 h before sunset as convection collapses. Note that, according to WMO and FAO (2016), a steady wind

speed of greater than 4 m/s will tend to prevent convection. However, this statement has not been confirmed by other sources.

Recent studies using entomological radar have enabled us to visualize individual insects from great distances and to scan huge volumes very rapidly, which contribute much to our understanding of insect migration (Chapman *et al.*, 2003; Drake & Reynolds, 2012). In the 1970s, vertical-looking insect monitoring radar (VLR) was developed as a new tool for monitoring high-altitude insect migration. By contrast to the early entomological scanning radar, VLR can provide information about the displacement speed and direction, heading orientation, size and shape of targets. Therefore, VLR has the capacity for the more precise identification of the target because it is a more powerful tool. Furthermore, VLR systems allow continuous and autonomous monitoring of pest migrations by computer, making it feasible to carry out routine monitoring with VLRS (Zhang *et al.*, 2012). Chandra *et al.* (2010) performed Doppler velocity measurements from insects occupying the lowest 2 km of the boundary layer during the summer months aiming to map the vertical velocity component of the convective boundary layer. Bell *et al.* (2013) derived average aerial densities and displacement speeds of insects in the daytime convective atmospheric boundary layer using VLR. They found that average insect densities decrease with increasing wind speed and increase with increasing air temperatures, and also that the relationship between displacement speed and density was negative. Both average speeds and densities were predicted remotely from a site over 100 km away. By late morning and afternoon, when insects are migrating in a well-developed convective atmosphere at high altitudes, they become much more difficult to predict remotely than during the early morning and at lower altitudes (Bell *et al.*, 2013).

Trap height versus trajectory height

To date, there have been very few studies that have investigated the vertical frequency of thrips species in the atmosphere. Using aircraft trapping, Glick (1939) collected Thysanoptera (winged adult specimens) in the upper atmosphere. However, his experiment covered only a few elevation levels, namely 60 m (33 specimens), 150 m (no specimens), 300 m (12 specimens), 600 m (five specimens), 900 m (three specimens), 1500 m (two specimens) and over 1500 m (one specimen). These data may only provide a schematic picture on the vertical dispersion of the thrips species. Nevertheless, they suggest that these insects are most frequent up to 600 m AGL, whereas their occurrence above 1500 m is incidental. This may confirm our decision that only two back-trajectory heights were used in the study 500 and 1500 m arrival heights, respectively.

However, the question arises of why we should use the above-mentioned back trajectories, if the thrips are most frequent below 100 m. We should add here that (i) there is always a difference between the amounts of insects oriented for local flights (they are much more numerous) and insects taking off for long-range transport. (ii) In some species, there may be a great variation in the migration range, even within an aphid clone. For example, Lewis and Taylor (1964) found that Thripidae and Phlaeothripidae were most abundant in the air near midday or in the early afternoon, and their flight curves were usually symmetrical about the most favoured time. (iii) The vertical occurrence

of the various species may be different [as an example, based on the aircraft experiment of Glick (1939), among 11 thrips species *Liothrips caryae* most frequently occurred at 60 and 300 m, *Neurothrips magnafemoralis* occurred at 900 and 1500 m, whereas *Haplotrips graminis* was present over 1500 m, respectively]. (iv) At lower altitudes, as a result of the higher friction, the transport component (i.e. passive displacement of the insects by the winds) has a much smaller weight (i.e. has a much smaller role) in the resulting displacement of the insect compared with high altitudes and vice versa. Overall, for long-range transport wind speed, increasing in the function of the height, is a better carrier (Lewis, 1973).

Thrips records in the function of the trap height

It is important to recall that there were 24 days in one of the examined years (2002) (Fig. 3), when the numbers of *S. tenuipennis* and *Z. figuratus* were high. The fact that two thrips species were recorded in high numbers leads to the presumption that they survived and established a small population in that year. For *Z. figuratus*, both males and females were caught. Even *S. tenuipennis* could also have multiplied and established a population, although no males were present, because this species, similar to some other *Thysanoptera* spp., may multiply by parthenogenesis (Jenser, 1982; zur Strassen, 2003).

The suction height of the trap may also be an important factor. According to Johnson (1969), a suitable height for collecting flying Thysanoptera is around 6 m AGL. In an earlier study (Jenser, 1973), a suction trap was used at this height for the autumn mass flight observation of *Frankliniella intonsa* (Thysanoptera: Thripidae). Teulon and Penman (1996) used the suction trap at a height of 7.5 m AGL to determine whether suction traps would be useful for monitoring the diversity and flight activity of some Thripidae species. The height of our trap (12 m AGL) differed slightly from those mentioned in the above studies (Jenser, 1973; Teulon & Penman, 1996) for detecting actively migrating insects or local populations in certain years.

Origin of the captured thrips species: long-range transport or local greenhouses?

Originally, based on daily observations, 51 flight days were detected. From this data set, there were eight trapping days (15.7%), for which a section of at least one of the two back-trajectories arriving at Hódmezővásárhely at 0000 UTC fell into the sector south of the latitude 40°N and between the longitudes 20°W and 20°E; namely, North Africa, the known natural habitat area of the captured species. A detailed analysis revealed that an African origin could be excluded for two species, namely *Caliothrips* and *F. schultzei*, because air masses did not originate or did not pass over North Africa on the above trapping days. For the other two species (*S. tenuipennis*, *Z. figuratus* males and *Z. figuratus* females), only lower percentages (12%, 13% and 25%) of such events were observed. Other back trajectories, coming from the Atlantic area and the Mediterranean, are much more common for all species. Live *Thysanoptera* spp. may reach the target area not only from the source area of a given

back trajectory, but also from any source areas along the back trajectory in the intermediate regions. In this way, if these insects come from a nearer source area to the target area, they have a better chance of staying alive. However, there is little chance that they reach the target station alive from Africa, through the long-distance transport.

Despite the lack of data in the literature on the accurate population distribution of *Z. figuratus* and *S. tenuipennis* in Europe, our results based on the HYSPLIT transport and dispersion model suggest that the captured thrips species might occur in several parts of Europe. Because the biology and life style of the predatory *S. tenuipennis* and the phytophagous *Z. figuratus* have not yet been clarified, further studies are needed to determine whether these species have already been settled down in Hungary, as well as in the Atlantic area and the Mediterranean Europe.

Although *Z. figuratus* was described by zur Strassen (1968) in association with *L. sinuatum* flowers in Morocco; it does not necessarily mean that this species is capable of proliferating or feeding on this plant. Otherwise, *L. sinuatum* has been cultivated for many years as an annual ornamental flower in Europe, such as in the Netherlands (Nordhuis, 1995) and Hungary (Nagy, 1991). Other data are unavailable on the further occurrence or appearance of *Z. figuratus* in the world. Regarding *F. schultzei*, it has a very wide distribution and is mainly found in tropical and subtropical areas throughout the world. In Europe, it was observed only in greenhouses with tropical circumstances in Denmark, Netherland, England and Spain (Vierbergen & Mantel, 1991; Schmidt & Frey, 1995; Trdan *et al.*, 2003; zur Strassen, 2003). These greenhouse observations occurred much earlier (zur Strassen, 2003) than our observations and those populations have already died out. Therefore, they cannot be related to established populations observed by the suction trap. In addition, so far, *F. schultzei* has not occurred in Hungary. There is small likelihood of the capability of this species for establishing itself because the suction trap caught only three specimens during the 3-year investigation period. The situation is similar for *Caliothrips* sp.: here, it is assumed that this subtropical species escaped from a local greenhouse.

The captured *Caliothrips* male is very similar or identical to *C. floridensis*, although this species is known from the female only (B. G. Vierbergen, personal communication). Because only males of *Caliothrips* were trapped, identification was possible on the genus level. Without the presence of females, thrips cannot be determined on species level. The related specimens were determined as belonging to *Caliothrips* genus. However, having only knowledge of the genus is not sufficient to clarify the country of origin and the host plants of the related *Caliothrips* species. These specimens may belong to an undescribed North-African species (G. Jenser, personal communication). In this case, without any reliable identification, it is sufficient to identify this species as *Caliothrips* spp. (G. Jenser, personal communication).

We assume that thrips from greenhouses in the Hódmezővásárhely area could settle more easily and possibly build up new populations there. Males usually fly better and can move longer distances than females, and so perhaps these two males may simply have escaped from a nearby greenhouse (B. G. Vierbergen, personal communication).

Conclusions

In the present study, we report the first occurrence of *S. tenuipennis* and *Z. figuratus* in the European continent. In addition, these species together with *Caliothrips* sp. and *F. schultzei* are first detected and hence are all new species for the Hungarian fauna. The present study has focused on the long-range transport of thrips using 3D back-trajectory analysis based on HYSPLIT transport and dispersion model for Europe.

Small insects, such as Thysanoptera, have a chance to colonize new areas through long-distance transport in the case of favourable climatic conditions. Surprisingly, there is quite a low chance of the long-distance transport of the captured Thysanoptera species from their known habitat, North Africa to the target area on the study days. The majority of the trapped Thysanoptera species possibly originated through active migration or long-distance dispersal from existing but hidden populations from local or nearby European source areas. Various source areas were more frequently detected from the Atlantic, the Mediterranean, the East-European steppic biogeographical region and the Black Sea area. These findings taken together suggest that other still unexplored habitats of these species might also exist in Europe, especially in the Atlantic area and the Mediterranean. From these possible European habitats, thrips species could be successively dispersed by both long-distance transport and migration. Nonetheless, we cannot exclude the possibility that these species might breed much closer to the suction trap than we have previously assumed. At the same time, regardless of whether they arrived from nearby habitats or from a long distance, we have confirmed their presence in the area of the trap. Therefore, more efforts should be taken to observe the establishment of new noxious species. In addition, it was shown that the application of the HYSPLIT method is a useful tool for studying the possible regional or long-distance transport of thrips species.

However, despite the lack of literature data on the detailed population distribution of *Z. figuratus* and *S. tenuipennis* in Europe, the results of the present study suggest that the captured thrips species could survive long-distance transport at low-level trajectories and establish new populations in a distant geographical area (i.e. in several parts of Europe). At the same time, further investigations are needed to determine whether the Thysanoptera species are capable of settling down in the Paleo-arctic region, including Hungary.

For reliable pest control, it is advisable to combine a knowledge of the local population with proper statistical methods to predict the migration of the species and to prepare appropriate plant protection measures in time. To ensure well-founded studies in the future, sound and long data sets with clearly identified species are needed.

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