



# Ragweed (*Ambrosia*) pollen transport and seed production in Finland during 1990–2022

Maria Louna-Korteniemi · Sanna Pätsi · Pasi Ahola ·  
Agneta Ekeboom · Maiju Kyyhkynen · Linnea Toiviainen ·  
Marika Viljanen · Annika Saarto

Received: 19 December 2024 / Accepted: 13 April 2025 / Published online: 5 May 2025  
© The Author(s) 2025

**Abstract** Common ragweed (*Ambrosia artemisiifolia*) is one of the most harmful alien invasive species in Europe. Ragweed pollen is a potent aeroallergen, and can travel long distances in the atmosphere. In this research we studied pollen samples collected in Turku, Finland, during 1990–2022, to identify when ragweed pollen was first transported to the country and how frequently it has happened since, how much pollen has been transported to the country yearly, and whether it is possible to observe trends in airborne ragweed pollen occurrence in Finland during the past decades. We show that (1) ragweed pollen has been transported to Finland since the 1990's, significantly earlier than previously thought, and (2) the long-distance transport episodes have often been more intense in the recent years. Ragweed pollen transports occur in the late summer or in the autumn, thus lengthening the pollen season in Finland. We also describe a case study where we show that ragweed is able to produce mature viable seeds in Finland. Our conclusion is that the significance of ragweed as an aeroallergen in Finland is increasing, and thus the situation needs to be regularly monitored.

**Keywords** Ragweed · *Ambrosia artemisiifolia* · Invasive alien species · Aeroallergen · Climate change

## 1 Introduction

Allergenic pollen season in Europe is characterized by deciduous trees flowering in the spring, grasses (Poaceae) from late spring to early autumn, and weeds such as mugworts (*Artemisia* spp.) and ragweeds (*Ambrosia* spp.) from late summer to autumn. Common ragweed (*Ambrosia artemisiifolia* L., Asteraceae; henceforth referred to as ragweed) is an annual, herbaceous, wind-pollinated plant native to North America, but invasive around the world, especially in Europe (Bassett & Crompton, 1975; Essl et al., 2015; Smith et al., 2013). It is a short-day plant, with flowering governed by photoperiod: flowering is induced after summer solstice when the day-length has shortened sufficiently (Allard, 1943, 1945; Deen et al., 1998a; Leiblein-Wild & Tackenberg, 2014). After ripening, ragweed seeds will enter a dormant state and require specific conditions to break the dormancy (Baskin & Baskin, 1977, 1980; Bazzaz, 1970).

Ragweed grows in anthropogenic environments in a wide range of open habitats associated with frequent soil disturbance, such as cultivated fields, roadsides and urban wastelands, and is highly invasive around the world in areas with temperate, continental climates (Bassett & Crompton, 1975; Bullock et al., 2012; Essl et al., 2015; Montagnani et al., 2017;

---

M. Louna-Korteniemi (✉) · S. Pätsi · P. Ahola ·  
M. Kyyhkynen · L. Toiviainen · M. Viljanen · A. Saarto  
Biodiversity Unit, University of Turku, Turku, Finland  
e-mail: amlouna@gmail.com

A. Ekeboom  
Palynological Laboratory, Swedish Museum of Natural  
History, Stockholm, Sweden

Smith et al., 2013). It is a noxious weed that can grow up to 250 cm high, it causes significant crop losses in agriculture, and its pollen is a potent aeroallergen causing respiratory problems and asthma; thus, the species has harmful impacts on human health, agriculture and economy (Bullock et al., 2012; Essl et al., 2015; Montagnani et al., 2017, 2023; Smith et al., 2013).

One ragweed plant produces an average of  $1.19 \pm 0.14$  billion pollen grains per year, and the pollen production correlates with the size of the plant (Fumanal et al., 2007). Ragweed pollen is highly allergenic and a significant health hazard both in North America and in the areas where the species is invasive (Bassett & Crompton, 1975; Arbes et al., 2005; Oswald & Marshall, 2008; Bullock et al., 2012; Smith et al., 2013; Salo et al., 2014; Essl et al., 2015; Montagnani et al., 2017).

The incidence of ragweed allergy has increased in Europe in the past decades (Bullock et al., 2012) and sensitization to ragweed has been proposed to increase by over 100% in the next few decades (Lake et al., 2016). Geographical differences in sensitization rates are high, and the choice of methods in studying sensitization rates creates variation between different studies (NHANES III; Arbes et al., 2005; NHANES, 2005–2006; Bousquet et al., 2007; Heinzerling et al., 2009; Bullock et al., 2012; Ruëff et al., 2012; Salo et al., 2014; Grewling et al., 2018, Stepalska et al., 2020 and references therein).

Various threshold values for ragweed pollen that are likely to induce allergy symptoms have been mentioned in several studies, usually ranging from 5 pollen grains per  $m^3$  of air (pollen/ $m^3$ ) daily average up to 20 pollen/ $m^3$ , but both lower and higher threshold values have also been proposed (Solomon, 1984; Comtois & Gagnon, 1988; Juhász, 1995, according to Makra et al., 2005; Makra et al., 2005; Bullock et al., 2012; Stepalska et al., 2020 and references therein). However, in a systematic review by Steckling-Muschack et al. (2021) no universal clinical threshold could be identified, and the authors concluded that sensitivity to ragweed pollen is strongly dependent on the individuals.

### 1.1 Ragweed distribution in Europe

In Europe, ragweed was first recorded in botanical gardens in the eighteenth century (Chauvel et al.,

2006; Essl et al., 2015). In nature, its early invasive history began in the nineteenth century when it was inadvertently introduced into Europe with imported agricultural products from North America (Essl et al., 2015; Montagnani et al., 2017, 2023; Smith et al., 2013). It began spreading more rapidly around the mid-twentieth century by repeated introductions and the process of naturalization, and has now colonized large areas in South-Eastern, Southern and Central Europe (Bullock et al., 2012; Chauvel et al., 2006; Essl et al., 2015; Montagnani et al., 2017, 2023; Smith et al., 2013). It is also invasive in many parts of Asia, Australia, Africa and South America (Cherez-Ojeda et al., 2024; Montagnani et al., 2017, 2023; Prank et al., 2013; Smith et al., 2013).

The spreading mechanisms of ragweed (both from native sources and from invaded areas) include dispersal through contaminated seed for crops, contaminated bird seeds, transport along roads and on agricultural machinery, and—with minor importance—natural seed dispersal e.g., by birds or wind (Bullock et al., 2012; Chapman et al., 2016; Chauvel et al., 2006; Essl et al., 2015; Lemke et al., 2019).

Temperature is an important limiting factor for the spread of ragweed (Cunze et al., 2013; Essl et al., 2015). The seedlings are sensitive to frost, and it is widely believed that in the northern reaches of the distribution area the first autumn frosts terminate the flowering and kill the plants before the seeds mature, if the plants even have time so start flowering (Allard, 1943; Deen et al., 1998b; Bullock et al., 2012; Essl et al., 2015; Petrova, 2019). However, there are some indications that the frost tolerance of mature plants may be slightly better than often thought. According to Dahl et al. (1999), the killing frost for ragweed is  $-5$  °C.

In Europe, ragweed's main area of distribution lies in the southern parts of Eastern and Central Europe, with largest populations especially in the Rhône valley (France), the Pannonian plains (Hungary), Po valley (Italy), Croatia and Serbia, and smaller established populations in, e.g., Belgium, the Netherlands, Germany and Poland (Bullock et al., 2012; Buters et al., 2015; Essl et al., 2015 and references therein). The species is also taking a foothold in the Nordic and Baltic countries. In Denmark, ragweed is systematically flowering although its ability to produce mature seeds has been uncertain (Skjøth et al., 2009; Ministeriet for

Fødevarer, Landbrug og Fiskeri, 2010). However, Bullock et al. (2012) report that it is spreading there from established areas. In Southern Sweden, a few cases have been reported during the 1990's when, during warm years, ragweed produced germinative seeds (Dahl et al., 1999), but, according to Scalone et al. (2016), there were no established populations in Sweden in 2016, as the plants did not have time to produce seeds before they were killed by frost. In Latvia, ragweed plants are observed yearly and the number of observations is rising, but there is no information about their possible seed production (Titane & Sozinova, 2023). Saar et al. (2000) reported that ragweed could produce seeds in Lithuania but not in Estonia, and in 2016 the situation in Estonia remained unchanged (Elvisto et al., 2016). Thus, the northern populations are mostly ephemeral and dependent on repeated seed introductions (Cunze et al., 2013; Dahl et al., 1999; Saar et al., 2000; Smith et al., 2013). However, some of the information available on ragweed occurrence and reproduction at the northern reaches of its distribution area is somewhat outdated, and newer assessments on the situation may be needed.

The current distribution of ragweed is smaller than its potential range, and several studies have predicted that the range will shift northwards and uphill in the future due to the ongoing naturalization process, climate change, seed dispersal and changes in land-use, aided by phenotypic plasticity and adaptive potential (e.g., Battlay et al., 2023; Cunze et al., 2013; Essl et al., 2015; Gallien et al., 2016; Gentili et al., 2021; Leiblein-Wild et al., 2016; Rasmussen et al., 2017; Scalone et al., 2016; Storkey et al., 2014).

Anthropogenic climate change has already altered the biosphere. The global surface temperature in 2011–2020 was ca. 1.1 °C higher than during 1850–1900, climate zones have shifted polewards, the growing season has lengthened, and there are observable changes in weather patterns and precipitation. Globally, warming in the long term (2081–2100) is projected to be from 1.0 °C in the best-case scenario (SSP1-1.9), to 5.7 °C in the worst-case scenario (SSP5-8.5). (IPCC, 2021.) The higher latitudes are expected to experience more warming than the southern regions (Lee et al., 2021), and the ragweed distribution area is expected to spread northwards under all climate scenarios (Cunze et al., 2013; Essl et al., 2015; Rasmussen et al., 2017; Storkey et al., 2014).

Warmer autumns and longer growing season will lengthen the pollen season (Ziska et al., 2011).

Different aspects of climate change, such as elevated CO<sub>2</sub> and elevated temperature, enhance the photosynthesis of ragweed and affect its growth, spread, flowering phenology, pollen and seed production and the allergenicity of pollen, but there may be differences in how different ecotypes react to the changes in their environment (Cheng et al., 2023; Gentili et al., 2019; Hamaoui-Laguel et al., 2015; Lake et al., 2016; Leiblein-Wild & Tackenberg, 2014; Montagnani et al., 2023; Rauer et al., 2020; Stinson et al., 2017; Wayne et al., 2002; Ziska & Beggs, 2012 and references therein). Abiotic factors that remain constant even in a changing climate, such as photoperiod, also pose challenges to species' capabilities to spread northwards and to adapt to a changing climate (Saikkonen et al., 2012). For short-day plants such as ragweed this is especially important.

## 1.2 Ragweed in Finland

Several studies have shown that ragweed pollen grains can be transported over long distances in the atmosphere (Belmonte et al., 2000; Cecchi et al., 2007; Smith et al., 2008; Kasprzyk et al., 2011; Šikoparija et al., 2013; Makra et al., 2016; Weger et al., 2016; Bilińska et al., 2017; Stepalska et al., 2020). Thus, ragweed pollen may cause allergic symptoms and sensitization even outside of the species' distribution area. Finland is located in the north of Europe, but even so, ragweed pollen is occasionally observed in the air with the routine monitoring of airborne pollen. To date, the first mention of long-distance transported (LDT) ragweed pollen in Finland is from 2005 (Saarinen & Jantunen, 2017), when ragweed pollen was detected at several measuring stations in central and northern Finland.

Ragweed is botanically classified in Finland as an ephemeral alien, i.e., a taxon that has not been able to persist or create populations (Kurtto et al., 2019), unlike Montagnani et al. report (2017), and officially classified as an “invasive alien to be monitored” (Niemiuvuo-Lahti, 2012). According to the Finnish Biodiversity Information Facility (<https://laji.fi>), a few to a few dozens of plant individuals are reported around the country every year, mostly in gardens and near bird feeding sites, but also on roadsides and wastelands. Observational bias may affect

our knowledge on the sites of ragweed occurrence in Finland, as the reports are often provided by garden and nature enthusiasts and not verified by experts, and gardens and bird feeding sites are one of the more typical places where people tend to make nature observations. An important route for ragweed seeds to Finland seems to be via birdseed, as reflected by the sites where they frequently occur, but this has not been systematically studied, and as the numbers of ragweed individuals are small, strong inferences on the routes are hard to make. Until recently it has been thought that ragweed is not able to reproduce in Finland as the first autumn frosts terminate the growing season before the plants have time to produce mature seeds (Kurtto, s.a.; Essl et al., 2015).

Local ragweed plants are so few and so far apart in Finland that they do not contribute to the overall pollen levels. However, the transported ragweed pollen may pose an allergy risk at least to some individuals, although little is known of its significance for autumnal allergy symptoms in Finland.

### 1.3 Purpose of the study

Although LDT ragweed pollen does occasionally reach Finland, its significance as part of the late pollen season and airborne allergenic load in the country has not been systematically studied. Information on ragweed phenology in the northern conditions in

Finland is also scant. The aim of this study is to fill that void, to clarify the picture of the occurrence of ragweed pollen in Finland from the early 1990's to the early 2020's, and to acquire more information on ragweed seed production in Finland via a case study.

The main study questions are: (a) since when and how often has ragweed pollen been transported to Finland, (b) how much pollen has been transported to the country yearly, (c) can ragweed produce mature seeds in Finland?

## 2 Materials and methods

### 2.1 Long-distance pollen transport

We analyzed air samples collected with Hirst-Burkard volumetric spore sampler (Hirst, 1952) in Turku, Southwest Finland, between 1990 and 2022, in the months of August, September, and October (Fig. 1).

At different times during the study period, the sampler was located on two different roofs at the University of Turku (UTU; 60.45521028N, 22.28512644E), all within 100 m from each other. Until 2012, the sampler was located 50 m above sea level (15 m above ground level), 2012–2016 42 m above sea level (10 m above ground level), and from 2016 onwards 51 m above sea level (16 m above ground level). The samplings –2012 and 2016–22 are

**Fig. 1** The locations from where pollen data was analyzed in the present study (Turku, Finland), and the locations from where it was used as an aid in identifying possible LDT days in Finland (Kuopio in Finland, Stockholm and Borlänge in Sweden, and Tallinn, Jõhvi and Kuressaare in Estonia)



from the same roof; the difference in height is due to structural changes of the roof and the setting of the sampler (to the rail), the site of the trap on the roof was moved by approx. 5–10 m. The tapes from the sampler had been cut into pieces so that each piece equaled one day (24 h; henceforth “sample”). The pieces were mounted on microscopic slides with Gelvatol. All the samples had been previously analyzed at UTU as part of the standard pollen monitoring routine, in which pollen grains are counted with a light microscope using 400× magnification on 48 random fields on the microscopic slides (Mäkinen, 1981). For the present study, we analyzed the entire collection area of the slides (14 mm×48 mm) with a light microscope using 200× magnification, and identified and counted all ragweed pollen grains. The number of pollen grains was converted to the daily average pollen concentration per cubic meter of air (pollen/m<sup>3</sup>).

Due to limited resources, it was not possible to analyze all the samples in the August–October time-frame between 1990 and 2022. Consequently, we applied the following methods to identify days with likely long-distance transport episodes (LDTs). We analyzed all the samples that fulfilled one or more of the following criteria:

- (a) Ragweed pollen had been detected in Turku or Kuopio with the standard monitoring routine described above. Kuopio is a city in Eastern Finland (Fig. 1), and was chosen as a reference point as it is part of the routine pollen monitoring network in Finland, and as ragweed pollen transported from Eastern Europe may occasionally have been detected there, even when it was not detected in Turku in Western Finland;
- (b) Non-specified Asteraceae pollen had been detected in Turku or Kuopio with routine monitoring: during the 1990’s and early 2000’s ragweed pollen was not routinely identified to the genus level but to family level Asteraceae. Therefore, some ragweed pollen may have been recorded as Asteraceae;
- (c) Ragweed pollen had been detected in the air at least at one of the following nearby aerobiological stations: Stockholm and Borlänge in Sweden, or Jõhvi, Kuressaare and Tallinn in Estonia (Fig. 1), based on the data available at European Aeroallergen Network (EAN). These were selected as reference sites due to their relative proximity to Turku and as airmasses moving from south to north will likely reach at least one of them before reaching Turku;
- (d) High amount of non-specified Asteraceae pollen was detected in different aerobiological stations in Sweden (selected with the same criteria as above) during 1990–1999, as during that time some ragweed pollen may have been recorded as Asteraceae.

After analyzing the samples identified using the above criteria, we analyzed all the previous and following samples in relation to the samples when ragweed pollen was detected in Turku, until a sample with zero ragweed pollen was reached. This enabled us to pinpoint the start and end dates of each LDT episode. Furthermore, in order to control whether our screening methods were indeed able to find all or most of the LDT episodes, we analyzed all the samples in August and September from the year 2017. The year 2017 was chosen as control because during the process of analyses we noticed that the same criteria indicated markedly less potential LDT days for 2017 than for 2018–2022. After analyzing the samples that were indicated by the criteria, we also found that the number of LDT days in 2017 was considerably lower than in 2018–2021. We wanted to ascertain that the differences between the years reflected the actual pollen situation, and were not the result of inadequate or biased criteria.

Some of the samples, especially the older ones, exhibited signs of deterioration, and, in some cases, it was difficult or impossible to analyze the entire collection area of the microscopic slide. These partly damaged samples were excluded from the calculations of daily pollen concentrations, and in cases where no ragweed pollen was found on the preserved part of the sample, it was also excluded from the analyses of LDT days. If ragweed pollen was detected on the preserved part of the sample, that day was treated as an LDT day, even though its daily pollen concentration could not be calculated. Consequently, 28 samples were excluded from the calculations of concentrations, 23 samples were excluded from the study completely, and 5 partially degraded samples containing ragweed pollen were treated as LDT days.

We analyzed 494 days in total. The number of days analyzed per year varied from 0 (1998) to 62 (2017). From 1998 no samples were analyzed, as we could

not identify any possible LDT days using the criteria described above. The number of days analyzed from 2017 was higher than from any other year, as we analyzed all the samples from August to September, and not just the samples for possible LDT days that were indicated by the criteria described above.

## 2.2 Case study: seed germination in Finland

The case study was conducted in Turku area. The climate is hemiboreal, characterized by warm summers and cold winters, subgroup *Dfb* in the Köppen climate classification system (Kottek et al., 2006). In August 2021, we observed by chance five naturally growing ragweed plants at a roadside wasteland in Auranlaakso, Kaarina, near the border of Turku (60.4684 N, 22.353 E). The plants were not sown there for the purpose of this study, but had grown from seeds of unknown origin. We wanted to test the belief that ragweed is not able to produce mature seeds in Finland, and started to monitor the plants regularly. At the beginning of November, seeds were observed on the plants. 70 seeds were collected and a laboratory growth experiment was conducted to test their viability. It is worth noting that during the following winter the ragweed-infested site was destroyed by extensive roadwork and construction, and that no ragweed plants have been observed growing at the site in the following years.

Ragweed seeds become dormant upon maturation and require exposure to winter temperatures (stratification) to break the dormancy. In our study, these conditions were simulated by conducting the seed collection, storage, wet-stratification and growth experiment based on methods and results described in previous studies on ragweed life cycles, seed dormancy or germination. (See e.g., Bazzaz, 1970; Picket & Baskin, 1973; Willemsen, 1975; Baskin & Baskin, 1980; Leiblein-Wild et al., 2014; Fogliatto et al., 2019.)

## 3 Results

### 3.1 Long-distance pollen transport

No ragweed pollen was detected in the majority of the analyzed samples (Fig. 2), and when ragweed

pollen was present, the daily average concentrations were mostly low ( $< 5$  pollen/m<sup>3</sup>) (Fig. 3; Table 1). The number of LDT episodes per year varied from 0 to 5 (average 1.6), and the length of episodes varied from 1 to 13 days (average 3.2 days) (Fig. 4).

The first ragweed pollen grain reaching Finland was found in a sample collected in 1991 (Fig. 2; Table 1). The first LDT episode with more than one pollen grain per sample occurred in 1995, and the first episode that lasted more than one day occurred in 1996 (Fig. 4). The first episode with average daily pollen concentration exceeding the often-used low-end clinical threshold of 5 pollen/m<sup>3</sup> occurred in 1997 (12.2 pollen/m<sup>3</sup>) (Fig. 3; Table 1). This episode was also the longest until that point, lasting six days (Fig. 4).

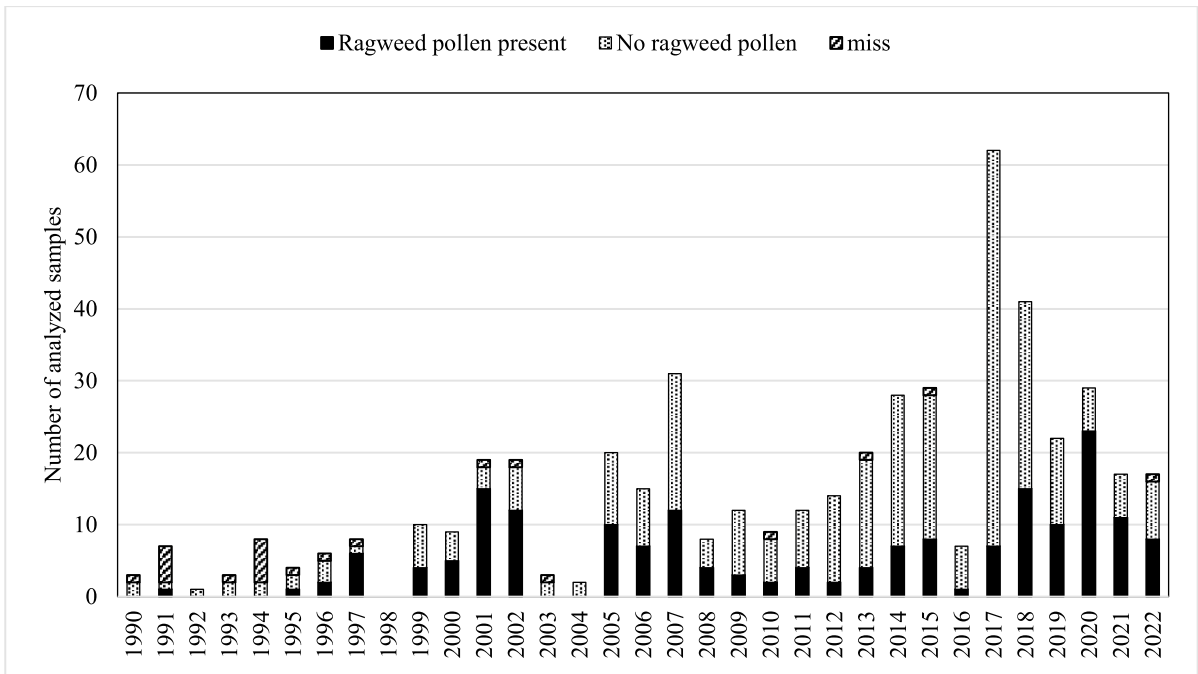
The average daily pollen concentration exceeded the threshold of 20 pollen/m<sup>3</sup> only four times during the study period, three of those occurring after 2018 (Table 1). The first time when pollen concentration exceeded 50 pollen/m<sup>3</sup> occurred in 2020.

The number of LDT days and the amount of transported pollen has varied a lot in the studied years, but the year 2020 was a record year in many ways. It had the maximum number of LDT days, with 23 days (Fig. 2), separated into two distinct episodes. 2020 also exhibited the highest daily pollen concentration, 64 pollen/m<sup>3</sup>, as well as the highest amount of transported pollen during the whole season (109 pollen/m<sup>3</sup>) (Fig. 3).

No ragweed pollen was found in 1990, 1992–1994, and 2003–2004 (Fig. 2). This may be partly due to the low number of analyzed samples, as our methods identified only a few possible days to be analyzed.

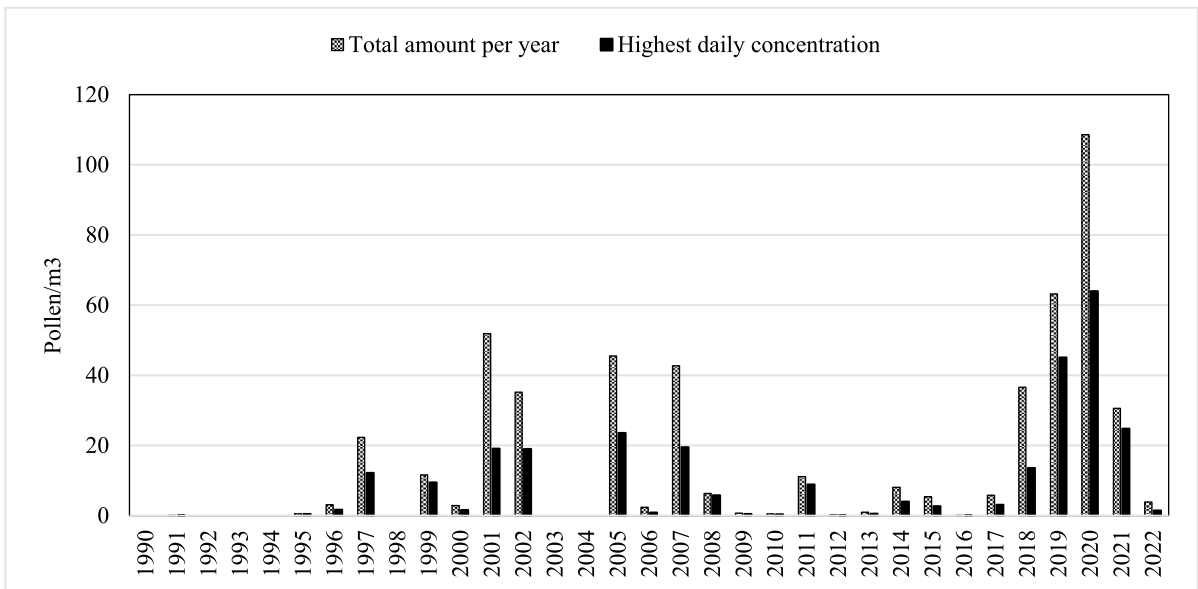
However, during the control year 2017, all the found LDT days were already indicated as potential LDT days by the selection criteria described above. No ragweed pollen was found from the samples that were not indicated as potential LDT days.

Most LDT days occurred between the last week of August and the end of September. The earliest calendar day with LDT pollen was 3 August (2014), and the latest 18 October (2018). However, in 2021, the first ragweed pollen grains of the year were captured with the routine monitoring already on July 21, but as July was not included in the present study, that observation is not part of this dataset.



**Fig. 2** The number of analyzed samples: Samples when ragweed pollen was detected (black bars); samples when no ragweed pollen was detected (dotted bars); and samples that could not be completely analyzed as part of the sample was either

missing or too degraded (“miss”; striped bars). No samples were analyzed from year 1998, as we could not identify any possible LDT days using the criteria described in the methods section



**Fig. 3** Total amount of LDT ragweed pollen in Turku per year (grey bars) and the highest daily pollen concentration per year (black bars) (pollen/m<sup>3</sup>)

**Table 1** The distribution of days with different daily ragweed pollen concentrations (pollen/m<sup>3</sup>) during the study period

Year	Concentration pollen/m <sup>3</sup>				
	0.1-4.9	5-9.9	10-19.9	20-50	> 50
1990	0	0	0	0	0
<b>1991</b>	<b>1</b>	0	0	0	0
1992	0	0	0	0	0
1993	0	0	0	0	0
1994	0	0	0	0	0
1995	1	0	0	0	0
1996	2	0	0	0	0
<b>1997</b>	<b>5</b>	0	<b>1</b>	0	0
1998	-	-	-	-	-
<b>1999</b>	<b>3</b>	<b>1</b>	0	0	0
2000	5	0	0	0	0
2001	10	0	<b>3</b>	0	0
2002	10	1	1	0	0
2003	0	0	0	0	0
2004	0	0	0	0	0
<b>2005</b>	<b>8</b>	0	<b>1</b>	<b>1</b>	0
2006	6	0	0	0	0
2007	9	1	2	0	0
2008	3	1	0	0	0
2009	3	0	0	0	0
2010	2	0	0	0	0
2011	2	1	0	0	0
2012	2	0	0	0	0
2013	4	0	0	0	0
2014	7	0	0	0	0
2015	8	0	0	0	0
2016	1	0	0	0	0
2017	7	0	0	0	0
2018	12	1	2	0	0
2019	8	1	0	1	0
<b>2020</b>	<b>20</b>	<b>1</b>	0	<b>1</b>	<b>1</b>
2021	8	0	0	1	0
2022	8	0	0	0	0

Bolding indicates the first year when the daily concentration fell within each range. No samples were analyzed from year 1998, as we could not identify any possible LDT days using the criteria described in the methods section

### 3.2 Case study: seed germination

In August 2021 we observed five ragweed plants growing at a roadside wasteland nearby Turku, and monitored them from August to November 2021. On 28 August the first male flowers were observed to be open and pollinating. On 19 September

several female flowers were open, but the exact date of the first female flowers opening is unknown. On 6 November, seeds were observed on three of the five plants.

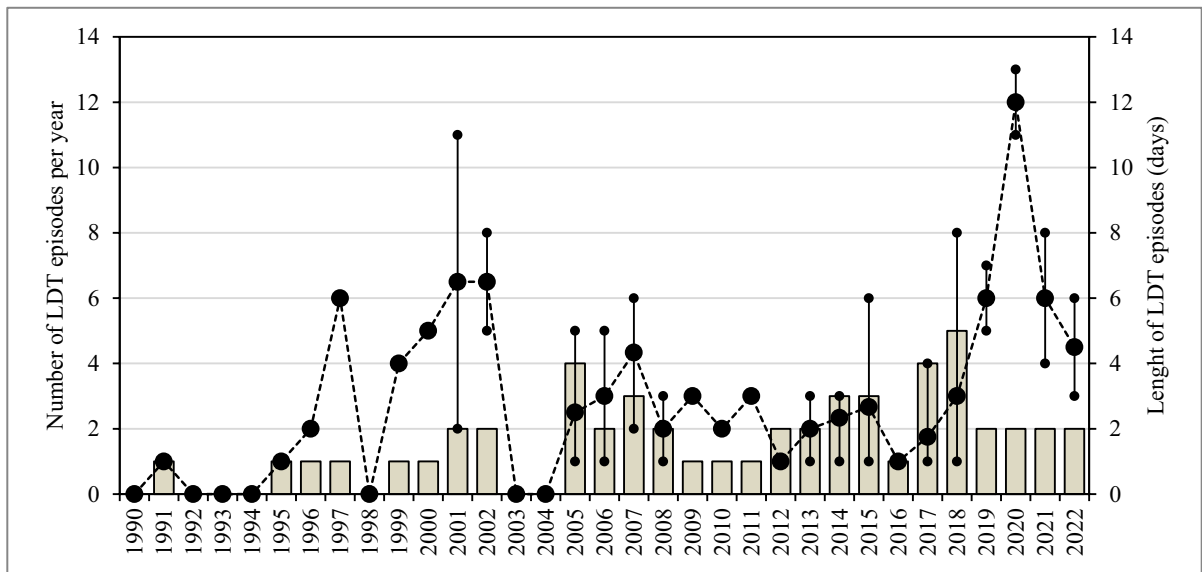
On 6 November, 52 seeds were collected, on 12 November the plants were visited again, and 18 more seeds were collected. In total 70 seeds were obtained. Only the seeds that seemed ripe or nearly ripe were collected. Most seeds on the plants were green, or soft and hollow. Green seeds were considered unripe and the soft seeds dead, and were not collected.

The observed plant individuals differed considerably in size and in the way they reacted to air temperatures as the autumn progressed. On 6 November, two of the largest individuals had already wilted and did not produce any seeds. Two other plants were mostly green and had produced some seeds, but were beginning to show early signs of wilting. One plant, the one producing most seeds, seemed to be thriving.

On 12 November, three of the five plants were dead, and the two remaining ones were wilting. From 13 November onwards the air temperatures remained mostly below freezing, there were no more seeds to collect, and the monitoring was discontinued.

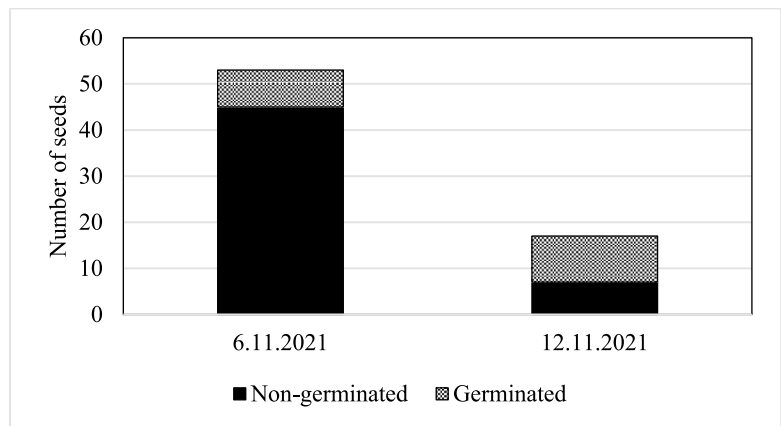
After the monitoring and seed collection, the growth experiment was started. The duration of the wet-stratification treatment was 12 weeks, after which the seeds were transferred to the climatic chamber. Some seeds germinated within two days of the transfer, and more continued to germinate during the next weeks. The experiment was terminated when no new seedlings had appeared during the previous two weeks. At that time, the seeds had been in the climatic chamber for approximately 6 weeks. It should be noted that a single seed provided an anomaly to this setup: This seed germinated already during wet-stratification treatment, after the treatment had continued for only 7 weeks. It was transferred to the climatic chamber already at that time, meaning that it spent in the chamber ca. 5 weeks longer than the other seeds.

Of the 52 seeds collected on 6 November, 7 seeds germinated (~13%). Of the 18 seeds collected on 12 November, 10 seeds germinated (~56%) (Fig. 5). The anomalous seed that germinated during the wet-stratification was from the set collected on 6 November.



**Fig. 4** Number of LDT episodes in (grey bars) in Turku, the average length of LDT episodes (large black dots) and the range between the shortest and longest episode of the year (small black dots)

**Fig. 5** Number of non-germinated (black bars) and germinated (grey bars) ragweed seeds by collection date. ~ 13% of the seeds collected on 6 November germinated, and ~ 56% of the seeds collected on 12 November germinated



## 4 Discussion

### 4.1 Long-distance pollen transport

We studied the incidence of LDT ragweed pollen in Finland during 1990–2022 by reanalyzing old samples collected in Turku, Finland, with Hirst-Burkard pollen traps. Our results show that ragweed pollen has been transported to Finland earlier than previously thought and that the most intense LDT episodes have occurred toward the end of the study era

(seen as the number of LDT days and the amount of transported pollen per year).

The earliest ragweed pollen grain transported to Finland that we found was in a sample from 1991. This pushes the occurrence of ragweed pollen in Finland back at least 14 years from what was previously known. Prior to our study, the first identified ragweed pollen grains were observed in Finland as part of routine monitoring (Mäkinen, 1981) in 2005, when LDT pollen reached Kuopio and Vaasa

in central Finland, and Oulu and Kevo (Utsjoki) in northern Finland (Saarinen & Jantunen, 2017).

When re-examining the routine monitoring data (i.e., tables of identified pollen but not the physical samples) for 2005, we confirmed that ragweed pollen was indeed recorded in Kuopio (25–27 August), Vaasa (25–26 August), Oulu (25–27 August), and Kevo (24–27 August), but not at the monitoring stations in southern Finland (Turku, Helsinki and Joutseno). In Helsinki, however, non-specified Asteraceae pollen was recorded 25–26 August, with concentrations 5 pollen/m<sup>3</sup> and 23 pollen/m<sup>3</sup>, respectively. It is rare for Asteraceae pollen, other than *Artemisia*, to reach such a high level as 23 pollen/m<sup>3</sup> in Finland at any time of the year, let alone so late in the summer, and we believe that this has most likely been ragweed pollen. Unfortunately, the physical samples do not exist anymore, so this cannot be ascertained. In the present study, we found that ragweed pollen also reached Turku 25–27 August, with daily concentrations 24 pollen/m<sup>3</sup>, 19 pollen/m<sup>3</sup> and < 1 pollen/m<sup>3</sup>. The measurements in Turku highlight the fact that small pollen amounts easily go undetected with routine pollen monitoring methodology (Mäkinen, 1981).

Our results show that, prior to the 2005 episode described above, pollen amounts above or around 10 ragweed pollen/m<sup>3</sup> daily average reached Turku already 5 September 2002 (19 pollen/m<sup>3</sup>), 21 September 2001 (19.1 pollen/m<sup>3</sup>), 6 September 1999 (9.5 pollen/m<sup>3</sup>) and 28 August 1997 (12.2 pollen/m<sup>3</sup>; the first episode in Finland with pollen concentration > 10 pollen/m<sup>3</sup>).

The same LDT episodes were observed also in Sweden, where ragweed pollen was recorded in Stockholm 5 September 2002 (72 pollen/m<sup>3</sup>), 21 September 2001 (20 pollen/m<sup>3</sup>) and 6 September 1999 (62 pollen/m<sup>3</sup>). 28 August 1997, no ragweed pollen was recorded in Sweden, but indetermined pollen was observed in Stockholm (11 pollen/m<sup>3</sup>), and Asteraceae pollen in Eskilstuna (41 pollen/m<sup>3</sup>) and Uppsala (22 pollen/m<sup>3</sup>). It is very likely that these pollen grains recorded as Asteraceae or as indetermined were actually ragweed. The first episode in Finland lasting more than one day occurred 28–29 August 1996 (1.4 pollen/m<sup>3</sup>), and 28 August 10 pollen/m<sup>3</sup> of Asteraceae pollen was recorded in Stockholm, which may also have been ragweed.

The above described LDT episodes in 1997 and 1996 were also recorded in Tartu and Kuressaare in Estonia (Saar et al., 2000).

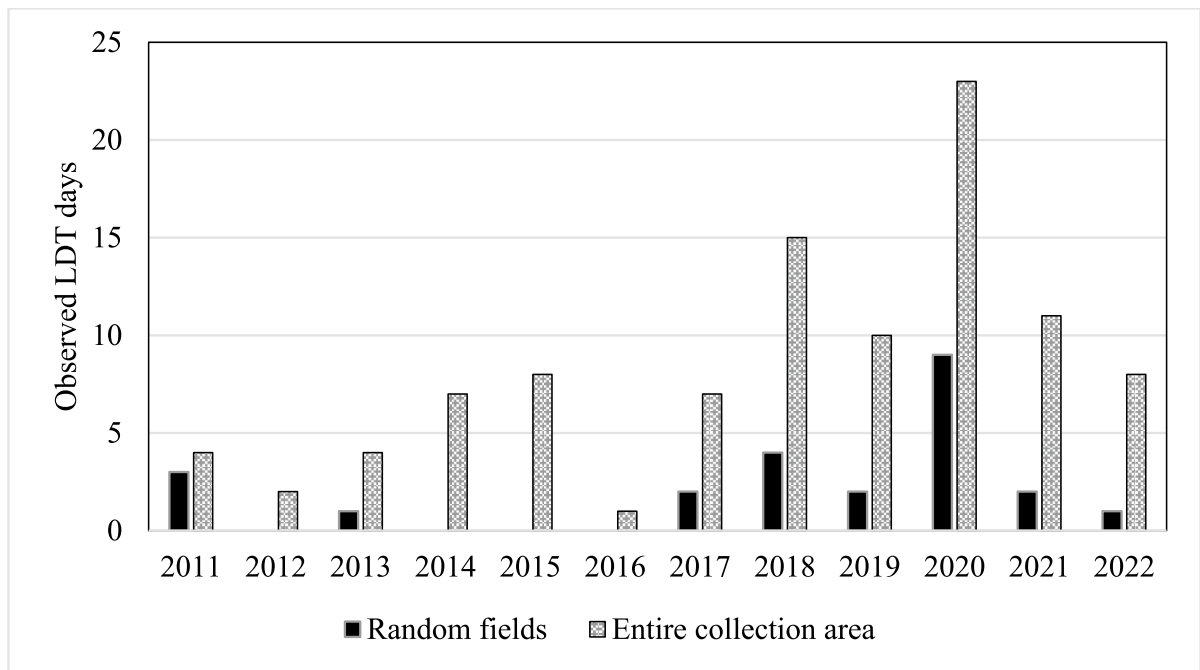
All in all, more LDT days were discovered in the present study where the entire collection area of the microscopic slide was analyzed, than with routine monitoring utilizing 48 random fields (Fig. 6).

There was a lot of interannual variation in the amount of LDT pollen. The amounts were relatively high in 2018–2021, and 2020 was a record year in many ways. During 2022, the last year of the dataset, the pollen amounts were again lower. Based on later routine monitoring data, ragweed pollen was scarce also during 2023, but a new record was made again in 2024, when the total amount of LDT pollen reached 231 pollen/m<sup>3</sup> (highest daily concentration 69 pollen/m<sup>3</sup>; analyzed according to Mäkinen, 1981).

As the sampler was located on two different roofs during the study period, it is possible that the different sampling heights may have had an effect on how much ragweed pollen was sampled. The amounts measured during 2012–2016, when the sampler was located lower, were quite small (highest daily count 4 pollen/m<sup>3</sup>, 20 September 2014). However, these amounts did not differ markedly from the amounts measured on the other roof, as the daily counts were mostly below 5 pollen/m<sup>3</sup> throughout the entire study period.

It was not possible to analyze all the days in August–October 1990–2022. Also, the clues we used for identifying potential LDT days for the analysis were more scattered the further back in time we go during the study period, and fewer days were analyzed from the 1990's than from the 2010's. Some of the older microscopic slides were partly degraded and analyzing them was difficult. Thus, it is possible that some minor LDT episodes were left out, and finding less transported pollen during the 1990's may partly be a result of a collection bias. However, we are confident that the majority of the LDT days were discovered.

One must also consider whether it is meaningful to treat days with pollen concentrations of 1 pollen/m<sup>3</sup> or below as LDT days. As ragweed can grow and some individuals also pollinate in Finland, it is possible that some of the ragweed pollen on the tapes may be from local sources. However, local plants are rare, and the days with pollen concentrations at or below 1 pollen/m<sup>3</sup> are the most numerous within the dataset,



**Fig. 6** Number of observed LDT days when using the random fields method of the routine monitoring system (light grey bars), and when analyzing the entire collection area of the microscopic slides (dark grey bars)

so we believe that most of the detected ragweed pollen is transported to the country from elsewhere. No correlations or causal relationships between the occurrence of LDT pollen and environmental factors were examined in this study. However, our observations on the amounts of transported pollen fit the picture of what is known of ragweed spread and changes in its pollen production and pollen transports under the changing climate, other anthropogenic factors, and the naturalization process (Cheng et al., 2023; Gentili et al., 2019; Hamaoui-Laguel et al., 2015; Lake et al., 2016; Leiblein-Wild & Tackenberg, 2014; Montagnani et al., 2023; Rauer et al., 2020; Stinson et al., 2017; Wayne et al., 2002; Ziska & Beggs, 2012 and references therein). As the distribution area is expected to shift northwards in the future, new pollen sources closer to Finland may increase both the amount of LDT pollen and the number and frequency of LDT episodes reaching the country. More ragweed growing in the source areas and the increases in pollen production may also lead to more pollen to be transported.

Back trajectory analyses would provide important information on the source areas from where ragweed

pollen is transported to Finland, and they are a crucial next step in further studies on this subject. It would be highly useful to track possible changes in the source areas over the years. Knowledge on possible changes in ragweed populations or its pollen production in the source areas, and on the factors driving these changes (e.g., changes in land use, or in the weather patterns under climate change) might help to predict future trends in ragweed pollen transports to Finland.

There are no studies estimating how many people in the general population of Finland are sensitized to ragweed pollen. According to Burbach et al. (2009), 2.4% of the routine out-patients at Helsinki University Hospital with allergic symptoms were sensitized to ragweed. However, people sensitized to mugworts (*Artemisia vulgaris*, *A. campestris* and other *Artemisia* species) pollen may be especially susceptible to show symptoms when exposed to ragweed pollen (Asero et al., 2006, 2014; Cecchi et al., 2010; Grewling et al., 2018; Ruëff et al., 2012). It is still unresolved how much of this is due to cross-reactivity and how much is caused by co-sensitization, at least from the viewpoint of clinical practice (Asero et al., 2014; Canis et al., 2012). Common mugwort, or simply

mugwort (*A. vulgaris*), is a late-flowering plant native to Finland and its pollen is considered one of the major outdoor allergens in the country. According to Heinzerling et al. (2009), mugwort sensitization rate in Finland is 17.6% within the atopic population. In North Karelia, 16.9% of randomly selected school-children showed positive sIgE-results to mugwort allergens and 7.3% reacted to skin prick tests (Pekkarinen et al., 2007). The mothers of the same children showed slightly different numbers: 6.1% gave positive sIgE test results and 9.0% reacted to skin prick tests. According to Jantunen and Saarinen (2008) there are approximately 100 000 people sensitized to mugwort in Finland (~1.9% of the population). These numbers are estimates, but based on them tens of thousands of people in Finland may react to transported ragweed pollen.

According to our study, ragweed pollen is transported to Finland in late summer and early autumn, the majority of it in late August and early September. Usually, as observed with the routine pollen monitoring, the peak of mugwort flowering is reached at the end of July or the first half of August. This means that ragweed pollen reaches Finland at the end of the mugwort season, or well after mugwort flowering is already over, thus lengthening the overall pollen season in Finland. However, the ragweed pollen concentrations measured in Finland are small in comparison to concentrations elsewhere in Europe. The daily mean values are usually < 5 pollen/m<sup>3</sup>, only occasionally exceeding 20 pollen/m<sup>3</sup>, and as yet have never exceeded 100 pollen/m<sup>3</sup>. In the more heavily infested areas in Europe the daily mean concentrations can reach several hundreds of pollen grains per cubic meter of air (e.g., Makra et al., 2016; Stepalska et al., 2020; Melnychenko et al., 2021).

Autumnal allergic symptoms in Finland are usually attributed to airborne fungal spores, such as *Cladosporium* spp. and *Alternaria* spp., as the spore concentrations of these genera in the air are at their highest in the late summer and in the early autumn (e.g., Koivikko et al., 1972, 1976; Rantio-Lehtimäki et al., 1985). It would be interesting to study the interaction between the occurrence of fungal spores and ragweed pollen in the air, as ragweed pollen is typically transported to Finland during the same time period when fungal spores are abundant. At least during the days when ragweed pollen concentrations in the air exceed 5 pollen/m<sup>3</sup> it may also cause allergic

symptoms on some individuals. LDT ragweed pollen can also be accompanied by fungal spores as well as anthropogenic air pollutants (Grewling et al., 2019), and the co-occurrence of allergenic pollen and fungal spores in the air may increase the severity of allergic symptoms and complicate their interpretation (Myszkowska et al., 2023).

#### 4.2 Seed germination in Finland

Our observations and growth experiment showed that, in favorable conditions, ragweed is able to produce viable seeds in Finland.

The development of ragweed plants and the timing of their flowering is an interplay of photoperiod, temperature and the accumulation of heat sum (Bullock et al., 2012; Cunze et al., 2013; Deen et al., 1998b; Essl et al., 2015). Ragweed flowering is said to be induced when the duration of daylight has shortened to ~14 h (Deen et al., 1998a; Bullock et al., 2012), though other studies indicate that earlier flowering is possible (Essl et al., 2015; Leiblein-Wild & Tackenberg, 2014; Magyar et al., 2022). Milakovic et al. (2014) assume the time between flowering and seed ripening to be 4–6 weeks, and the same numbers are reported by Essl et al. (2015). According to Beres (1994) the time for seed maturation is longer, 64 days on average (~9 weeks), and Scalone et al. (2016) report an even longer time of 10–12 weeks. Knolmayer et al. (2024) write that ragweed needs 40–60 days (~6–9 weeks) after fertilization to produce fully ripe seeds, but the source they give (Makra et al., 2015) does not mention the time needed for seed ripening. Thus, the origin of the statement in Knolmayer et al. remains unknown, but the numbers do fall between the other estimates given in other studies. In southern parts of Europe, the flowering usually starts in late July or early August (Essl et al., 2015), and the seeds ripen sometime in September. In Finland, lower temperatures slow down the development of the plants, and the flowering usually starts in the beginning of September (personal observations). The seeds would then be predicted to ripen between mid-October and mid-November. In our case study, the first female flowers were observed 19 September, and seeds were collected on 6 and 12 November, giving them roughly 7–8 weeks to ripen on the plants.

It is believed that the first autumn frosts end the period for the development of viable ragweed seeds

(e.g., Essl et al., 2015; Solomon, 1984), but in our case study some of the seeds were collected after several night frosts, and they actually germinated better than the seeds that were collected before the coldest temperatures. This observation suggests that the first frosts may not immediately terminate the development of viable seeds, giving the plants a longer-than-previously-thought window to reproduce in the northern parts of their distribution area. Also, the frost tolerance of ragweed plants may be slightly better than often reported. Several researches state that the first frosts kill ragweed (Deen et al., 1998b; Essl et al., 2015; Ziska et al., 2011), but Dahl et al. (1999) reported that plants die in temperatures below  $-5^{\circ}\text{C}$ . Our observations in the field confirm that some ragweed individuals can tolerate at least approximately  $-4^{\circ}\text{C}$  before they die. In southern Finland, it is possible that the autumn temperatures keep mostly above freezing well into November, giving the seeds more time to mature.

During our study, some nighttime frosts occurred in September, October and November, measured in Turku airport,  $\sim 6.5$  km from the location where the ragweed plants of this study were found (Fig. 7).

The coldest temperatures before collecting seeds were  $-3.9^{\circ}\text{C}$  (19 October) and  $-3.3^{\circ}\text{C}$  (24 October). These temperatures were measured 2 m above ground; at ground level where the plants grow the temperatures are usually  $1\text{--}2^{\circ}\text{C}$  lower. At least three of the plants seemed to survive these frosts. During the first days of November, the temperatures remained several degrees above  $0^{\circ}\text{C}$ . After collecting the first set of seeds on 6 November, the nighttime temperatures fell below  $0^{\circ}\text{C}$  for three nights in a row, ranging from  $-2.0$  to  $-8.6^{\circ}\text{C}$ . The latest, on 9 November, was the coldest night during the study period, and killed all the remaining plants. The second set of seeds was collected three days after this.

There was a marked difference between the germination rates of the seeds collected on different days, with the germination rate of the seeds collected later being higher than that of the seeds collected earlier. Considering the possible reasons for this result, there were three obvious differences between the different sets of seeds. First, the later set of seeds were attached to the plants approximately one week longer than the earlier set; second, during that extra week in the field the later seeds were exposed to more frosts than the



**Fig. 7** Miniand maximum daily temperatures during 1.8.–15.11.2021, measured in Turku airport,  $\sim 6.5$  km from the location where the ragweed plants of this study were found. These

measurements were made 2 m above ground; at ground level the temperatures are typically  $1\text{--}2^{\circ}\text{C}$  lower (Finnish Meteorological Institute, weather observations, CC BY 4.0.)

earlier; and third, between harvesting and the wet stratification, the later set of seeds was stored one week less than the earlier set.

It is possible for ragweed seeds to continue ripening on cut branches after harvesting (Karrer & Pixner, 2012). But as most of the seeds in our study seemed already ripe at the time of collection, as they were detached from the branches completely, and as the set of seeds that was collected later germinated better than the earlier set, we believe the possibility of post-harvest ripening does not affect our results in any meaningful way. If frost terminated the development of viable seeds, the opposite result in the germination rates would have been expected – the germination rate of the later set of seeds would have been lower – but this was not the case. It also seems unlikely that the difference in storage time would have had such an influence in the germination rates. Then the possible explanation that remains is that the set of seeds that were collected later may have germinated better than the earlier set of seeds because they had had more time to mature on the plants in the field.

However, as the number of plants and seeds in our case study was low, no definite conclusions can be drawn from the seed germination experiment. Especially the number of seeds collected later was so small, that the relative abundances of the germinated and non-germinated seeds within that set may have been the result of chance. Hall et al. (2021) also show that the results of seed viability tests are affected not only by the properties of the seeds, but also by the testing methods and laboratories. However, our results are interesting, and indicate that further systematic studies with more plant individuals and a larger number of seeds would be useful in examining how much frost the plants tolerate at the end of the growing season, how frost affects ragweed seed maturation and germination, and how much variation is there between individuals considering these aspects.

It has been shown that there is phenological variation between plants from different populations, both in North America and Europe: plants from more

northerly populations tend to flower earlier than plants from southerly areas, and may be pre-adapted to the thermal conditions and light-environment in the higher latitudes, which gives the seeds more time to mature in the autumn, and may facilitate the spread of ragweed to Fennoscandia (Basset & Crompton, 1975; Solomon, 1984; Scalone et al., 2016; Krallmann et al., 2018; McGoey et al., 2020). Bullock et al. (2012) report that the minimum necessary mean July temperature for ragweed to naturalize in an area is 15–20 °C. During the normal period 1991–2020 defined by Finnish Meteorological Institute (FMI) the mean July temperature in Turku was 17.6 °C.

In 2021, the average temperature in July was 20.3 °C. Also, June and October 2021 were warmer than average, although August and September were cooler (Table 2). The warm temperatures in June and July 2021 may have enhanced the vegetative growth of the ragweed plants that were observed in the present study, and the warm temperature in October may have given the seeds more time to mature.

Our study shows that one reproductive barrier preventing ragweed from naturalizing in Finland can be overcome, at least during years with especially favorable temperatures. Due to the warming caused by climate change, conditions favoring the reproduction of ragweed in Finland are becoming more common. McGoey and Stinchcombe (2021) also show that ragweed will be able to respond quickly to selection pressures in changing environments. Thus, it is important to monitor ragweed plants and their possible seed production in Finland so that measures to prevent the species from forming established populations in Finland can be undertaken as soon as possible, if needed.

## 5 Conclusions

In our study we find that ragweed pollen has occurred in Finland since early 1990's, much earlier than previously thought, and that the LDT episodes have been

**Table 2** Average temperatures in Turku during the normal period 1991–2020 and in 2021 (Finnish Meteorological Institute, weather observations, CC BY 4.0.)

	Average temperature °C in Turku						
	Year	Jun	Jul	Aug	Sep	Oct	Nov
1991–2020	5.8	14.7	17.8	16.6	11.8	6.2	2.1
2021	6.8	18.4	20.3	15.2	9.7	8.1	1.4

more intense in the recent years. Our germination experiment shows that ragweed plants are able to produce viable seeds during the warmest autumns in Finland, and that freezing temperature during the maturation of seeds may not be an immediate killing factor neither for the plants nor their seeds.

With climate change the significance of ragweed as an aeroallergen in Finland may be increasing. It is also possible that ragweed may eventually naturalize as part of the Finnish flora as the plants are able to produce viable seeds during warm autumns.

Further studies are needed, and it is important to continue monitoring ragweed pollen transports and possible seed production in Finland.

**Acknowledgements** The authors wish to thank the Research Council of Finland for funding this research as part of the All-Impress project; TOP-Säätiö for funding the PhD research of M. Louna-Korteniemi; Estonian Environmental Research Centre for access to the Estonian pollen data; J. Korteniemi for the map of locations of pollen measurements and for thorough proofreading of the manuscript; A.-M. Pessi for her insights and comments; K. Saikkonen for good discussions; and M. Mäkelä for his valuable comments around the subject of mugwort.

**Author contributions** M.L.-K. Conceptualization, methodology, data analysis, writing – original draft and the main manuscript, review and editing, funding acquisition. S.P. Conceptualization, methodology, material preparation, data collection, writing – review and editing. P.A., M.K., L.T. and M.V. Material preparation and data collection. A.E. Data collection, writing – review and editing. A.S. Conceptualization, methodology, writing – review and editing, funding acquisition, supervision. All authors read and approved the final manuscript.

**Funding** Open Access funding provided by University of Turku (including Turku University Central Hospital). This work was supported by the Research Council of Finland (329217) and TOP-säätiö (20200637).

**Data availability** Pollen data used in this study is available on request by contacting Pollen forecasting, University of Turku.

## Declarations

**Competing interests** The authors declare no competing interests.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The

images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

## References

- Allard, H. A. (1943). The North American ragweeds and their occurrence in other parts of the world. *Science*, 98(2544), 292–294.
- Allard, H. A. (1945). Flowering behavior and natural distribution of the eastern ragweeds (*Ambrosia*) as affected by length of day. *Ecology*, 26(4), 387–394. <https://doi.org/10.2307/1931660>
- Arbes, S. J., Jr., Gergen, P. J., Elliot, L., & Zeldin, D. C. (2005). Prevalences of positive skin test responses to 10 common allergens in the US population: Results from the third National Health and Nutrition Examination Survey. *Journal of Allergy and Clinical Immunology*, 116, 337–383.
- Asero, R., Bellotto, E., Ghiani, A., Aina, R., Villalta, D., & Citterio, S. (2014). Concomitant sensitization to ragweed and mugwort pollen: Who is who in clinical allergy? *Annals of Allergy, Asthma & Immunology*, 113, 307–313. <https://doi.org/10.1016/j.anai.2014.06.009>
- Asero, R., Wopfner, N., Gruber, P., Gadermaier, G., & Ferreira, F. (2006). *Artemisia* and *Ambrosia* hypersensitivity: Co-sensitization or co-recognition? *Clinical and Experimental Allergy*, 36, 658–665. <https://doi.org/10.1111/j.1365-2222.2006.02477.x>
- Baskin, J. M., & Baskin, C. C. (1977). Role of Temperature in the Germination Ecology of Three Summer Annual Weeds. *Oecologia*, 30, 377–382. <https://doi.org/10.1007/BF00399768>
- Baskin, J. M., & Baskin, C. C. (1980). Ecophysiology of secondary dormancy in seeds of *Ambrosia artemisiifolia*. *Ecology*, 61(3), 475–480. <https://doi.org/10.2307/1937410>
- Bassett, I. J., & Crompton, C. W. (1975). The biology of Canadian weeds.11. *Ambrosia artemisiifolia* L. and *A. psilostachya* DC. *Canadian Journal of Plant Science*, 55, 463–476. <https://doi.org/10.4141/cjps75-072>
- Battlay, P., Wilson, J., Bieker, V. C., Lee, C., Prapas, D., Petersen, B., Craig, S., van Boheemen, L., Scalone, R., de Silva, N. P., Sharma, A., Konstantinović, B., Nurkowski, K. A., Rieseberg, L. H., Connallon, T., Martin, M. D., & Hodgins, K. A. (2023). Large haploblocks underlie rapid adaptation in the invasive weed *Ambrosia artemisiifolia*. *Nature Communications*, 14, 1717. <https://doi.org/10.1038/s41467-023-37303-4>
- Bazzaz, F. A. (1970). Secondary dormancy in the seeds of the common ragweed *Ambrosia artemisiifolia*. *Bulletin of the Torrey Botanical Club*, 97(5), 302–305. <https://doi.org/10.2307/2483650>

- Belmonte, J., Vendrell, M., Roure, J. M., Vidal, J., Botey, J., & Cadahia, A. (2000). Levels of *Ambrosia* pollen in the atmospheric spectra of Catalan aerobiological stations. *Aerobiologia*, *16*, 93–99. <https://doi.org/10.1023/A:1007649427549>
- Beres, I. (1994). New investigations on the biology of *Ambrosia artemisiifolia* L. *Mededelingen Faculteit Landbouwkundige En Toegepaste Biologische Wetenschappen, Universiteit Gent*, *59*(3b), 1295–1297.
- Bilińska, D., Skjøth, C. A., Werner, M., Kryza, M., Malkiewicz, M., Krynicka, J., & Drzeniecka-Osiadacz, A. (2017). Source regions of ragweed pollen arriving in south-western Poland and the influence of meteorological data on the HYSPLIT model results. *Aerobiologia*, *33*, 315–326. <https://doi.org/10.1007/s10453-017-9471-9>
- Bousquet, P.-J., Chinn, S., Janson, C., Kogevinas, M., Burney, P., & Jarvis, D. (2007). Geographical variation in the prevalence of positive skin tests to environmental aeroallergens in the European Community Respiratory Health Survey I. *Allergy*, *62*, 301–309. <https://doi.org/10.1111/j.1398-9995.2006.01293.x>
- Bullock, J.M., Chapman, D., Schafer, S., Roy, D., Girardello, M., Haynes, T., Beal, S., Wheeler, B., Dickie, I., Phang, Z., Tinch, R., Čivić, K., Delbaere, B., Jones-Walters, L., Hilbert, A., Schrauwen, A., Prank, M., Sofiev, M., Niemelä, S., et al. (2012). *Assessing and controlling the spread and the effects of common ragweed in Europe*. Final report: ENV.B2/ETU/2010/0037: Natural Environment Research Council, UK. 456 pp.
- Burbach, G. J., Heinzerling, L. M., Röhnelt, C., Bergmann, K.-C., Behrendt, H., & Zuberbier, T. (2009). Ragweed sensitization in Europe – GAZLEN study suggests increasing prevalence. *Allergy*, *64*, 664–665. <https://doi.org/10.1111/j.1398-9995.2009.01975.x>
- Buters, J. T. M., Alberternst, B., Nawrath, S., Wimmer, M., Traidl-Hoffmann, C., Starfinger, U., Behrendt, H., Schmidt-Weber, C., & Bergmann, K. C. (2015). *Ambrosia artemisiifolia* (ragweed) in Germany. Current presence, allergologic relevance and containment procedure. *Allergo Journal International*, *24*, 108–120. <https://doi.org/10.1007/s40629-015-0060-6>
- Canis, M., Becker, S., Gröger, M., & Kramer, M. F. (2012). IgE reactivity patterns in patients with allergic rhinoconjunctivitis to ragweed and mugwort pollens. *American Journal of Rhinology & Allergy*, *26*, 31–35. <https://doi.org/10.2500/ajra.2012.26.3698>
- Cecchi, L., Testi, S., Campi, P., & Orlandini, S. (2010). Long-distance transport of ragweed pollen does not induce new sensitizations in the short term. *Aerobiologia*, *26*, 351–352. <https://doi.org/10.1007/s10453-010-9164-0>
- Cecchi, L., Torrigiani Malaspina, T., Albertini, R., Zanca, M., Ridolo, E., Usberti, I., Morabito, M., Dall'Aglio, P., & Orlandini, S. (2007). The contribution of long-distance transport to the presence of *Ambrosia* pollen in central northern Italy. *Aerobiologia*, *23*, 145–151. <https://doi.org/10.1007/s10453-007-9060-4>
- Chapman, D. S., Makra, L., Albertini, R., Bonini, M., Páldy, A., Rodinkova, V., Šikoparija, B., Weryszko-Chmielewska, E., & Bullock, J. M. (2016). Modelling the introduction and spread of non-native species: International trade and climate change drive ragweed invasion. *Global Change Biology*, *22*, 3067–3079. <https://doi.org/10.1111/gcb.13220>
- Chauvel, B., Dessaint, F., Cardinal-Legrand, C., & Bretagnolle, F. (2006). The historical spread of *Ambrosia artemisiifolia* L. in France from herbarium records. *Journal of Biogeography*, *33*, 665–673. <https://doi.org/10.1111/j.1365-2699.2005.01401.x>
- Cheng, X., Frank, U., Zhao, F., Ruiz Capella, J., Winkler, B., Schnitzler, J.-P., Ghirardo, A., Bertić, M., Estrella, N., Durner, J., & Pritsch, K. (2023). Plant growth traits and allergenic potential of *Ambrosia artemisiifolia* pollen as modified by temperature and NO<sub>2</sub>. *Environmental and Experimental Botany*, *206*, Article 105193. <https://doi.org/10.1016/j.envexpbot.2022.105193>
- Cherez-Ojeda, I., Robles-Velasco, K., Ramon, G. D., et al. (2024). Ragweed in South America: The relevance of aerobiology stations in Latin America. *Aerobiologia*, *40*, 343–351. <https://doi.org/10.1007/s10453-024-09825-x>
- Comtois, P., & Gagnon, L. (1988). Concentration pollinique et fréquence des symptômes de pollinose: Une méthode pour déterminer des seuils cliniques. *Revue Française D'allergologie Et D'immunologie Clinique*, *28*(4), 279–286. [https://doi.org/10.1016/S0335-7457\(88\)80046-7](https://doi.org/10.1016/S0335-7457(88)80046-7)
- Cunze, S., Leiblein, M. C., & Tackenberg, O. (2013). Range expansion of *Ambrosia artemisiifolia* in Europe is promoted by climate change. *ISRN Ecology*, *2013*, 1–9. <https://doi.org/10.1155/2013/610126>
- Dahl, Å., Stranhede, S.-O., & Wihl, J. -Å. (1999). Ragweed—An allergy risk in Sweden? *Aerobiologia*, *15*, 293–297. <https://doi.org/10.1023/A:1007678107552>
- de Weger, L. A., Pashley, C. H., Šikoparija, B., Skjøth, C. A., Kasprzyk, I., Grewling, L., Thibaudon, M., Magyar, D., & Smith, M. (2016). The long distance transport of airborne *Ambrosia* pollen to the UK and the Netherlands from Central and south Europe. *International Journal of Biometeorology*, *60*, 1829–1839. <https://doi.org/10.1007/s00484-016-1170-7>
- Deen, W., Hunt, T., & Swanton, C. J. (1998a). Influence of temperature, photoperiod, and irradiance on the phenological development of common ragweed (*Ambrosia artemisiifolia*). *Weed Science*, *46*, 555–560. <https://doi.org/10.1017/S0043174500091098>
- Deen, W., Hunt, T., & Swanton, C. J. (1998b). Photothermal time describes common ragweed (*Ambrosia artemisiifolia* L.) phenological development and growth. *Weed Science*, *46*(5), 561–568. <https://doi.org/10.1017/S0043174500091104>
- Elvisto, T., Pensa, M., & Paluoja, E. (2016). Indigenous and alien vascular plant species in a northern European urban setting (Tallinn, Estonia). *Proceedings of the Estonian Academy of Sciences*, *65*(4), 431–441. <https://doi.org/10.3176/proc.2016.4.09>
- Essl, F., Biro, K., Brandes, D., Broennimann, O., Bullock, J. M., Chapman, D. S., Chauvel, B., Dullinger, S., Fumal, B., Guisan, A., Karrer, G., Kazinczi, G., Kueffer, C., Laitung, B., Lavoie, C., Leitner, M., Mang, T., Moser, D., Müller-Schärer, H., ... Follak, S. (2015). Biological Flora of the British Isles: *Ambrosia artemisiifolia*. *Journal of Ecology*, *103*, 1069–1098. <https://doi.org/10.1111/1365-2745.12424>

- Fogliatto, S., Milan, M., De Palo, F., & Vidotto, F. (2019). The effect of various after-ripening temperature regimens on the germination behaviour of *Ambrosia artemisiifolia*. *Plant Biosystems*, 154(2), 165–172. <https://doi.org/10.1080/11263504.2019.1578282>
- Fumanal, B., Chauvel, B., & Bretagnolle, F. (2007). Estimation of pollen and seed production of common ragweed in France. *Annals of Agricultural and Environmental Medicine*, 14, 233–236.
- Gallien, L., Thuiller, W., Fort, N., Boleda, M., Alberto, F. J., Rioux, D., et al. (2016). Is there any evidence for rapid, genetically-based, climatic niche expansion in the invasive common ragweed? *PLoS One*, 11(4), Article e0152867. <https://doi.org/10.1371/journal.pone.0152867>
- Gentili, R., Ambrosini, R., Augustinus, B. A., Caronni, S., Cardarelli, E., Montagnani, C., Müller-Schärer, H., Schaffner, U., & Citterio, S. (2021). High phenotypic plasticity in a prominent plant invader along altitudinal and temperature gradients. *Plants*, 10, 2144. <https://doi.org/10.3390/plants10102144>
- Gentili, R., Asero, R., Caronni, S., Guarino, M., Montagnani, C., Mistrello, G., & Citterio, S. (2019). *Ambrosia artemisiifolia* L. temperature responsive traits influencing the prevalence and severity of pollinosis: a study in controlled conditions. *BMC Plant Biology*, 19, 155. <https://doi.org/10.1186/s12870-019-1762-6>
- Grewling, L., Bogawski, P., Kryza, M., Magyar, D., Šikoparija, B., Skjøth, C. A., Udvardy, O., Werner, M., & Smith, M. (2019). Concomitant occurrence of anthropogenic air pollutants, mineral dust and fungal spores during long-distance transport of ragweed pollen. *Environmental Pollution*, 254, Article 112948. <https://doi.org/10.1016/j.envpol.2019.07.116>
- Grewling, L., Jenerowicz, D., Bogawski, P., Smith, M., Nowak, M., Frątczak, A., & Czarnecka-Operacz, M. (2018). Cross-sensitization to *Artemisia* and *Ambrosia* pollen allergens in an area located outside of the current distribution range of *Ambrosia*. *Advances in Dermatology and Allergology*, 35(1), 83–89. <https://doi.org/10.5114/ada.2018.73167>
- Hall, R. M., Urban, B., Skálová, H., Moravcová, L., Sölter, U., Starfinger, U., Kazinczi, G., van Valkenburg, J., Fenesi, A., Konstantinovic, B., Uludag, A., Lommen, S., & Karrer, G. (2021). Seed viability of common ragweed (*Ambrosia artemisiifolia* L.) is affected by seed origin and age, but also by testing method and laboratory. *Neobiota*, 70, 193–221. <https://doi.org/10.3897/neobiota.70.66915>
- Hamaoui-Laguel, L., Vautard, R., Liu, L., Solmon, F., Viovy, N., Khvorostyanov, D., Essl, F., Chuine, I., Colette, A., Semenov, M. A., Schaffhauser, A., Storkey, J., Thibaudon, M., & Epstein, M. M. (2015). Effects of climate change and seed dispersal on airborne ragweed pollen loads in Europe. *Nature Climate Change*, 5, 766–772. <https://doi.org/10.1038/nclimate2652>
- Heinzerling, L. M., Burbach, G. J., Edenharter, G., Bachert, C., Bindslev-Jensen, C., Bonini, S., Bousquet, J., Bousquet-Rouanet, L., Bousquet, P. J., Bresciani, M., Bruno, A., Burney, P., Canonica, G. W., Darsow, U., Demoly, P., Durham, S., Fokkens, W. J., Giavi, S., Gjomarkaj, M., et al. (2009). GA2LEN skin test study I: GA2LEN harmonization of skin prick testing: novel sensitization patterns for inhalant allergens in Europe. *Allergy*, 64, 1498–1506. <https://doi.org/10.1111/j.1398-9995.2009.02093.x>
- Hirst, J. M. (1952). An automatic volumetric spore trap. *Annals of Applied Biology*, 39(2), 257–265. <https://doi.org/10.1111/j.1744-7348.1952.tb00904.x>
- IPCC (2021). Summary for Policymakers. In: Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M.I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J.B.R., Maycock, T.K., Waterfield, T., Yelekçi, O., Yu, R., & Zhou, B. (eds.) *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. (2391 pp.) Cambridge University Press. <https://doi.org/10.1017/9781009157896.001>
- Jantunen, J., & Saarinen, K. (2008). *Pujo taajama-alueiden allergiakasvina*. Loppuraportti. Etelä-Karjalan Allergia-ja Ympäristöinstituutti. Joutseno. 31 pp. ISBN: 978-952-5156-52-2.
- Juhász, M. (1995). New results of aeropalynological research in Southern Hungary. *Hungarian Academy of Sciences Regional Committee Szeged*, 5, 17–30.
- Karrer, G., & Pixner, T. (2012). The contribution of post-harvest ripened ragweed seeds after cut for control. In: GEIB (eds.), *Neobiota* (p. 229). 7th European Conference on Biological Invasions.
- Kasprzyk, I., Myszkowska, D., Grewling, L., Stach, A., Šikoparija, B., Skjøth, C. A., & Smith, M. (2011). The occurrence of *Ambrosia* pollen in Rzeszów, Kraków and Poznań, Poland: Investigation of trends and possible transport of *Ambrosia* pollen from Ukraine. *International Journal of Biometeorology*, 55, 633–644. <https://doi.org/10.1007/s00484-010-0376-3>
- Knolmayer, B., Jócsák, I., Tállér, J., Keszthelyi, S., & Kazinczi, G. (2024). Common Ragweed—*Ambrosia artemisiifolia* L.: a review with special regards to the latest results in biology and ecology. *Agronomy*, 14, 497. <https://doi.org/10.3390/agronomy14030497>
- Koivikko, A., Mäkinen, Y., Rantio-Lehtimäki, A., & Kupias, R. (1976). *Aerobiologia ja allergia*. In (anon.), *Allergia-tutkimussäätiön vuosikirja 1976* (1st ed., pp. 14–19). Allergiatutkimussäätiö.
- Koivikko, A., Käpylä, M., & Mäkinen, Y. (1972). Siitepölyt ja sieni-itiöt allergioiden aiheuttajina. *Suomen Lääkärilehti*, 27, 1711.
- Kottek, M., Grieser, J., Beck, C., Rudolf, B., & Rubel, F. (2006). World Map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift*, 15(3), 259–263. <https://doi.org/10.1127/0941-2948/2006/0130>
- Kralemann, L. E. M., Scalone, R., Andersson, L., & Hennig, L. (2018). North European invasion by common ragweed is associated with early flowering and dominant changes in FT/TFL1 expression. *Journal of Experimental Botany*, 69(10), 2647–2658. <https://doi.org/10.1093/jxb/ery100>
- Kurtto, A. (s.a.). Marunatuoksukki – *Ambrosia artemisiifolia*. Suomen lajitietokeskus. Retrieved 9 March, 2022, from <https://laji.fi/taxon/MX.39794>.

- Kurtto, A., Lampinen, R., Piirainen, M., & Uotila, P. (2019). Checklist of the vascular plants of Finland. Suomen putkilokasvien luettelo. *Norrinia*, 34, 1–206.
- Lake, I. R., Jones, N. R., Agnew, M., Goodess, C. M., Giorgi, F., Hamaoui-Laguel, L., Semenov, M. A., Solomon, F., Storkey, J., Vautard, R., & Epstein, M. M. (2016). Climate change and future pollen allergy in Europe. *Environmental Health Perspectives*, 125(3), 385–391. <https://doi.org/10.1289/EHP173>
- Lee, J.-Y., Marotzke, J., Bala, G., Cao, L., Corti, S., Dunne, J.P., Engelbrecht, F., Fischer, E., Fyfe, J.C., Jones, C., Maycock, A., Mutemi, J., Ndiaye, O., Panickal, S., & Zhou, T. (2021). Future Global Climate: Scenario-Based Projections and Near-Term Information. In Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M.I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J.B.R., Maycock, T.K., Waterfield, T., Yelekçi, O., Yu, R., & Zhou, B. (Eds.), *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 553–672). Cambridge University Press. <https://doi.org/10.1017/9781009157896.006>
- Leiblein-Wild, M. C., Kaviani, R., & Tackenberg, O. (2014). Germination and seedling frost tolerance differ between the native and invasive range in common ragweed. *Oecologia*, 174, 739–750. <https://doi.org/10.1007/s00442-013-2813-6>
- Leiblein-Wild, M. C., Steinkamp, J., Hickler, T., & Tackenberg, O. (2016). Modelling the potential distribution, net primary production and phenology of common ragweed with a physiological model. *Journal of Biogeography*, 43, 544–554. <https://doi.org/10.1111/jbi.12646>
- Leiblein-Wild, M. C., & Tackenberg, O. (2014). Phenotypic variation of 38 European *Ambrosia artemisiifolia* populations measured in a common garden experiment. *Biological Invasions*, 16, 2003–2015. <https://doi.org/10.1007/s10530-014-0644-y>
- Lemke, A., Kowarik, I., & von der Lippe, M. (2019). How traffic facilitates population expansion of invasive species along roads: The case of common ragweed in Germany. *Journal of Applied Ecology*, 56, 413–422. <https://doi.org/10.1111/1365-2664.13287>
- Magyar, D., Novák, R., Udvardy, O., Páldy, A., Szigeti, T., Stjepanović, B., Hrga, I., Večenaj, A., Vucjić, A., Peroš Pucar, D., Šikoparija, B., Radišić, P., Škorić, T., Ščevková, J., Simon-Csete, E., Nagy, M., & Leelőssy, Á. (2022). Unusual early peaks of airborne ragweed (*Ambrosia L.*) pollen in the Pannonian Biogeographical Region. *International Journal of Biometeorology*, 66, 2195–2203. <https://doi.org/10.1007/s00484-022-02348-5>
- Mäkinen, Y. (1981). Random sampling in the study of microscopic slides. *Reports from the Aerobiology Laboratory, University of Turku*, 5, 27–43.
- Makra, L., Juhász, M., Béczi, R., & Borsos, E. (2005). The history and impacts of airborne *Ambrosia* (Asteraceae) pollen in Hungary. *Grana*, 44(1), 57–64. <https://doi.org/10.1080/00173130510010558>
- Makra, L., Matyasovszky, I., Hufnagel, L., & Tusnády, G. (2015). The history of ragweed in the world. *Applied Ecology and Environmental Research*, 13(2), 489–512. [https://doi.org/10.15666/aeer/1302\\_489512](https://doi.org/10.15666/aeer/1302_489512)
- Makra, L., Matyasovszky, I., Tusnády, G., Wang, Y., Csépe, Z., Bozóki, Z., Nyúl, L. G., Eröstyák, J., Bodnár, K., Sümeghy, Z., Vogel, H., Pauling, A., Páldy, A., Magyar, D., Mányoki, G., Bergmann, K.-C., Bonini, M., Šikoparija, B., Radišić, et al. (2016). Biogeographical estimates of allergenic pollen transport over regional scales: Common ragweed and Szeged, Hungary as a test case. *Agricultural and Forest Meteorology*, 221, 94–110. <https://doi.org/10.1016/j.agrformet.2016.02.006>
- McGoey, B. V., Hodgins, K. A., & Stinchcombe, J. R. (2020). Parallel flowering time clines in native and introduced ragweed populations are likely due to adaptation. *Ecology and Evolution*, 10, 4595–4608. <https://doi.org/10.1002/ece3.6163>
- McGoey, B. V., & Stinchcombe, J. R. (2021). Introduced populations of ragweed show as much evolutionary potential as native populations. *Evolutionary Applications*, 14, 1436–1449. <https://doi.org/10.1111/eva.13211>
- Melnichenko, H., Hrushka, V., & Ivanova, O. (2021). Dynamics of ragweed pollen concentration in the air of Ivano-Frankivsk. *Journal of Vasyl Stefanyk Precarpathian National University*, 8(4), 45–51. <https://doi.org/10.15330/jpnu.8.4.45-51>
- Milakovic, I., Fiedler, K., & Karrer, G. (2014). Management of roadside populations of invasive *Ambrosia artemisiifolia* by mowing. *Weed Research*, 54, 256–264. <https://doi.org/10.1111/wre.12074>
- Ministeriet for Fødevarer, Landbrug og Fiskeri, (2010). *Rapport over undersøgelse af vildtfugle-blandinger for indhold af bynkeambrosie frø (Ambrosia artemisiifolia L.) – vinter 2009–2010*. Ministeriet for Fødevarer, Landbrug og Fiskeri. Denmark. ISBN 978-87-7083-727-9.
- Montagnani, C., Gentili, R., & Citterio, S. (2023). Ragweed in the air: *Ambrosia L.* (Asteraceae) and pollen allergens in a changing world. *Current Protein and Peptide Sciences*, 24, 98–111. <https://doi.org/10.2174/1389203724666221121163327>
- Montagnani, C., Gentili, R., Smith, M., Guarino, M. F., & Citterio, S. (2017). The worldwide spread, success, and impact of ragweed (*Ambrosia* spp.). *Critical Reviews in Plant Sciences*, 36(3), 139–178. <https://doi.org/10.1080/07352689.2017.1360112>
- Myszkowska, D., Bogawski, P., Piotrowicz, K., Bosiacka, B., Grinn-Gofrón, A., Berger, U. E., Bonini, M., Ceriotti, V., Charalampopoulos, A., Galán, C., Gedda, B., Ianovici, N., Kloster, M., Oliver, G., Pashley, C. H., Pátsi, S., Pérez-Badia, R., Puc, M., Rodinkova, V., et al. (2023). Co-exposure to highly allergenic airborne pollen and fungal spores in Europe. *Science of the Total Environment*, 905(2023), Article 167285. <https://doi.org/10.1016/j.scitotenv.2023.167285>
- Niemivuo-Lahti, J. (ed.), (2012). *Kansallinen vieraslajistrategia*. Maa- ja metsätalousministeriö. 126 pp. ISBN 978-952-453-725-4
- Oswalt, M. L., & Marshall, G. D., Jr. (2008). Ragweed as an example of worldwide allergen expansion. *Allergy*,

- Asthma, and Clinical Immunology*, 4(3), 130–135. <https://doi.org/10.1186/1710-1492-4-3-130>
- Pekkarinen, P. T., von Hertzen, L., Laatikainen, T., Mäkelä, M. J., Jousilahti, P., Kosunen, T. U., Pantelejev, V., Vartiainen, E., & Haahtela, T. (2007). A disparity in the association of asthma, rhinitis, and eczema with allergen-specific IgE between Finnish and Russian Karelia. *Allergy*, 62, 281–287. <https://doi.org/10.1111/j.1398-9995.2006.01249.x>
- Petrova, S. E. (2019). Development of invasive weeds *Ambrosia artemisiifolia* L. and *A. trifida* L. (Asteraceae) in Moscow oblast. *Russian Journal of Biological Invasions*, 10(4), 370–381. <https://doi.org/10.1134/S207511719040088>
- Pickett, S. T., & Baskin, J. M. (1973). The role of temperature and light in the germination behavior of *Ambrosia artemisiifolia*. *Bulletin of the Torrey Botanical Club*, 100(3), 165–170. <https://doi.org/10.2307/2484628>
- Prank, M., Chapman, D. S., Bullock, J. M., Belmonte, J., Berger, U., Dahl, Å., Jäger, S., Kovtunen, I., Magyar, D., Niemelä, S., Rantio-Lehtimäki, A., Rodinkova, V., Šaulienė, I., Severova, E., Šikoparija, B., & Sofiev, M. (2013). An operational model for forecasting ragweed pollen release and dispersion in Europe. *Agricultural and Forest Meteorology*, 182–183, 43–53. <https://doi.org/10.1016/j.agrformet.2013.08.003>
- Rantio-Lehtimäki, A., Mäkinen, Y., & Pohjola, A. (1985). Seasonal variations in airborne fungus spore frequencies in Finland. *Reports from the Aerobiology Laboratory, University of Turku*. ISSN 0356-8598.
- Rasmussen, K., Thyrring, J., Muscarella, R., & Borchsenius, F. (2017). Climate-change-induced range shifts of three allergenic ragweeds (*Ambrosia* L.) in Europe and their potential impact on human health. *PeerJ*, 5, Article e3104. <https://doi.org/10.7717/peerj.3104>
- Rauer, D., Gilles, S., Wimmer, M., Frank, U., Mueller, C., Musiol, S., Vafadari, B., Aglas, L., Ferreira, F., Schmitt-Kopplin, P., Durner, J., Winkler, J. B., Ernst, D., Behrendt, H., Schmidt-Weber, C. B., Traidl-Hoffmann, C., & Alessandrini, F. (2020). Ragweed plants grown under elevated CO<sub>2</sub> levels produce pollen which elicit stronger allergic lung inflammation. *Allergy*, 76, 1718–1730. <https://doi.org/10.1111/all.14618>
- Ruëff, F., Przybilla, B., Walker, A., Gmeiner, J., Kramer, M., Sabanés-Bové, D., Küchenhoff, H., & Herzinger, T. (2012). Sensitization to common ragweed in southern bavaria: Clinical and geographical risk factors in atopic patients. *International Archives of Allergy and Immunology*, 159, 65–74. <https://doi.org/10.1159/000335192>
- Saar, M., Gudžinskas, Z., Ploompuu, T., Linno, E., Minkienė, Z., & Motiekaitytė, V. (2000). Ragweed plants and airborne pollen in the Baltic states. *Aerobiologia*, 16, 101–106. <https://doi.org/10.1023/A:1007670229308>
- Saarinen, K. & Jantunen, J. (2017). *Siitepölyä ilmassa! Allergiaa aiheuttavat siitepölyt Suomessa 1980–2015*. Etelä-Karjalan allergia- ja ympäristöinstituutti. Imatra. 101 pp.
- Saikkonen, K., Taulavuori, K., Hyvönen, T., Gundel, P. E., Hamilton, C. E., Vänninen, I., Nissinen, A., & Helander, M. (2012). Climate change-driven species' range shifts filtered by photoperiodism. *Nature Climate Change*, 2, 239–242. <https://doi.org/10.1038/nclimate1430>
- Salo, P. M., Arbes, S. J., Jaramillo, R., Calatroni, A., Weir, C. H., Sever, M. L., Hoppin, J. A., Rose, K. M., Liu, A. H., Gergen, P. J., Mitchell, H. E., & Zeldin, D. C. (2014). Prevalence of allergic sensitization in the U.S.: Results from the National Health and Nutrition Examination Survey (NHANES) 2005–2006. *Journal of Allergy and Clinical Immunology*, 134(2), 350–359. <https://doi.org/10.1016/j.jaci.2013.12.1071>
- Scalone, R., Lemke, A., Štefanić, E., Kolseth, A.-K., Rašić, S., & Andersson, L. (2016). Phenological variation in *Ambrosia artemisiifolia* L. facilitates near future establishment at northern latitudes. *PLoS ONE*, 11(11), Article e0166510. <https://doi.org/10.1371/journal.pone.0166510>
- Šikoparija, B., Skjøth, C. A., Alm Kübler, K., Dahl, Å., Sommer, J., Grewling, L., Radišić, P., & Smith, M. (2013). A mechanism for long distance transport of *Ambrosia* pollen from the Pannonian Plain. *Agricultural and Forest Meteorology*, 180, 112–117. <https://doi.org/10.1016/j.agrformet.2013.05.014>
- Skjøth, C. A., Petersen, H., Sommer, J., & Smith, M. (2009). Copenhagen: A harbinger for ragweed (*Ambrosia*) in Northern Europe under climate change? *IOP Conference Series: Earth and Environmental Science*, 6, Article 142031. <https://doi.org/10.1088/1755-1307/6/14/142031>
- Smith, M., Cecchi, L., Skjøth, C. A., Karrer, G., & Šikoparija, B. (2013). Common ragweed: A threat to environmental health in Europe. *Environment International*, 61, 115–126. <https://doi.org/10.1016/j.envint.2013.08.005>
- Smith, M., Skjøth, C. A., Myszkowska, D., Uruska, A., Puc, M., Stach, A., Balwier, Z., Chlopek, K., Piotrowska, K., Kasprzyk, I., & Brandt, J. (2008). Long-range transport of *Ambrosia* pollen to Poland. *Agricultural and Forest Meteorology*, 148, 1402–1411. <https://doi.org/10.1016/j.agrformet.2008.04.005>
- Solomon, W. R. (1984). Aerobiology of pollinosis. *Journal of Allergy and Clinical Immunology*, 74(4), 449–461. [https://doi.org/10.1016/0091-6749\(84\)90376-2](https://doi.org/10.1016/0091-6749(84)90376-2)
- Steckling-Muschack, N., Mertes, H., Mittermeier, I., Schutzmeier, P., Becker, J., Bergmann, K.-C., Böse-O'Reilly, S., Buters, J., Damialis, A., Heinrich, J., Kabesch, M., Nowak, D., Walser-Reichenbach, S., Weinberger, A., Zamfir, M., Herr, C., Kutzora, S., & Heinze, S. (2021). A systematic review of threshold values of pollen concentrations for symptoms of allergy. *Aerobiologia*, 37, 395–424. <https://doi.org/10.1007/s10453-021-09709-4>
- Stępańska, D., Myszkowska, D., Piotrowicz, K., Kluska, K., Chlopek, K., Grewling, L., Lafféřsová, J., Majkowska-Wojciechowska, B., Malkiewicz, M., Piotrowska-Weryszko, K., Puc, M., Rodinkova, V., Rybniček, O., Ščevková, J., & Voloshchuk, K. (2020). High *Ambrosia* pollen concentrations in Poland respecting the long distance transport (LDT). *Science of the Total Environment*, 736, Article 139615. <https://doi.org/10.1016/j.scitotenv.2020.139615>
- Stinson, K. A., Albertine, J. M., Seidler, T. G., Christine, A., & Rogers, C. A. (2017). Elevated CO<sub>2</sub> boosts reproduction and alters selection in northern but not southern ecotypes of allergenic ragweed. *American Journal of Botany*, 104(9), 1313–1322. <https://doi.org/10.3732/ajb.1700222>

- Storkey, J., Stratonovitch, P., Chapman, D. S., Vidotto, F., & Semenov, M. A. (2014). A process-based approach to predicting the effect of climate change on the distribution of an invasive allergenic plant in Europe. *PLoS One*, 9(2), Article e88156. <https://doi.org/10.1371/journal.pone.0088156>
- Titane, P.E., & Sozinova, O. (2023). Distribution of common ragweed (*Ambrosia artemisiifolia*) plant and pollen in Latvia and factors affecting them. *Current stage and future perspectives of bioaerosol research in Europe*. Book of abstracts. 81<sup>th</sup> International Scientific Conference of the University of Latvia 2023. 10 pp.
- Wayne, P., Foster, S., Connolly, J., Bazzaz, F., & Epstein, P. (2002). Production of allergenic pollen by ragweed (*Ambrosia artemisiifolia* L.) is increased in CO<sub>2</sub>-enriched atmospheres. *Annals of Allergy, Asthma & Immunology*, 88, 279–282. [https://doi.org/10.1016/S1081-1206\(10\)62009-1](https://doi.org/10.1016/S1081-1206(10)62009-1)
- Willemsen, R. W. (1975). Effect of stratification temperature and germination temperature on germination and the induction of secondary dormancy in common ragweed seeds. *American Journal of Botany*, 62(1), 1–5. <https://doi.org/10.1002/j.1537-2197.1975.tb12333.x>
- Ziska, L. H., & Beggs, P. J. (2012). Anthropogenic climate change and allergen exposure: The role of plant biology. *The Journal of Allergy and Clinical Immunology*, 129, 27–32. <https://doi.org/10.1016/j.jaci.2011.10.032>
- Ziska, L., Knowlton, K., Rogers, C., Dalan, D., Tierney, N., Elder, M. A., Filley, W., Shropshire, J., Ford, L. B., Hedberg, C., Fleetwood, P., Hovanky, K. T., Kavanaugh, T., Fulford, G., Vrtis, R. F., Patz, J. A., Portnoy, J., Coates, F., Bielory, L., & Frenzo, D. (2011). Recent warming by latitude associated with increased length of ragweed pollen season in central North America. *PNAS*, 108(10), 4248–4251. <https://doi.org/10.1073/pnas.1014107108>