

Comparison of the spectrum and quantity of airborne bioparticles above morphologically typical populations of *Ambrosia artemisiifolia* and those with reduced male flower production

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Abstract

In central Europe, where *Ambrosia artemisiifolia* L. is an invasive weed, several populations exhibiting an aberrant morphotype have been identified. This morphotype is primarily characterised by bractate racemes and the absence of staminate heads in the inflorescences, and it tends to occur at the edges of agricultural areas. Using spore traps positioned at three different heights (0, 50, and 150 cm), we compared the composition of the aerobiome above these aberrant populations with that of control populations displaying the typical morphology. *Ambrosia* pollen concentrations were lower above the aberrant populations, likely due to a higher proportion of pistillate and bisexual flowers. We also observed differences in the composition and abundance of airborne fungal spores, with certain phytopathogenic taxa more prominent above the aberrant populations. Notably, *Cryptophyllachora*, *Albugo*, and *Puccinia* may have a potential causative role in the development of the aberrant morphotype, although further research is required to confirm these associations.

1 Introduction

Ambrosia artemisiifolia L. (common ragweed), hereafter referred to as *Ambrosia* or ragweed, is an annual plant species native to North America, which has become one of the most problematic invasive alien species in Europe (Csontos et al., 2010; Afonin et al., 2018). International trade has facilitated its rapid spread across the continent, particularly through contaminated seed shipments (Chauvel et al., 2006). Due to its high reproductive potential and adaptability to disturbed habitats (Zhao et al., 2023), it is widely established in many parts of central and southern Europe, with expanding populations reported also in eastern and northern regions (Knolmajer et al., 2024).

Ambrosia poses significant ecological and socio-economic threats: it contributes to the decline of native biodiversity by outcompeting local flora (Sărățeanu et al., 2010; Csiszár et al., 2013), reduces agricultural productivity, especially of low-growing crops such as soybean (Weaver, 2001), and has serious implications for public health due to its highly allergenic pollen, which is a major cause of seasonal allergic rhinitis and asthma in sensitive individuals (Smith et al., 2013).

This monoecious species forms heads with approximately 10–100 male flowers, while solitary female flowers, sometimes clustered, are located in the axils of the upper leaves (Bassett and Crompton, 1975). As reported by Šaulienė and Veriankaitė Šaulys et al. (2012), a single ragweed plant can generate around 36,000 male flowers, with each anther containing approximately 4,000 pollen grains, resulting in a total pollen output of up to 7 billion grains per plant. In comparison, the threshold at which most individuals allergic to ragweed pollen begin to experience symptoms is only 20–30 pollen grains per m³ in Central Europe (Makra et al., 2005). The male heads are arranged in determinate spike-like terminal racemes, which together form a determinate panicle.

In recent years, several populations of *Ambrosia* with atypical morphological traits have been documented (Vidović et al., 2016). These individuals exhibit distorted or feminised terminal inflorescences and produce dry, mostly empty seeds. Such floral malformations are known in plants and

may arise due to genetic mutations (Mátyás et al., 2019; Pei et al., 2024), environmental stress (Müller et al., 2016; Gentili et al., 2018), or pathogen-induced hormonal imbalances (Harth et al., 2016; Minato et al., 2014; Himeno et al., 2011).

In Slovakia, we recently recorded several sites where *Ambrosia* individuals exhibited pronounced feminisation of terminal inflorescences, accompanied by a marked decline or total absence of male (pollen-producing) flower structures. These symptoms, which resemble pathogen-induced floral malformations observed in other plant species, raise the possibility that phytopathogenic agents may trigger such changes. Known causative organisms of similar plant syndromes include phytoplasmas (e.g., *Aster yellows* or *Stolbur*), bacteria, fungi, and insect or mite herbivores. For example, phytoplasmas are capable of manipulating host plant development by interfering with floral meristem identity genes, often leading to phyllody, virescence, or sterility (Pracros et al., 2006; Himeno et al., 2011; Minato et al., 2014). Similarly, certain fungal pathogens (e.g., *Ustilago* spp.) (Djamei and Kahmann et al., 2012), eriophyid mites (de Lillo et al., 2018), or insect herbivores can disrupt floral development through hormonal manipulation or physical damage to meristematic tissue (Rojas-Nossa et al., 2021; Wang et al., 2023).

The aetiology of this aberrant phenotype is currently unknown, though a phytopathogenic influence is suspected. Its exact identification would require comprehensive analyses of plant tissues, including the detection of potential pathogens and their associated insect or mite vectors, many of which may act as intermediate hosts. Given the reproductive modifications and potential pathogen involvement, it is possible to compare the composition and abundance of airborne bioparticles above the aberrant populations, compared to morphologically typical populations, from an aerobiological point of view. In doing so, we aim to narrow down the range of candidate phytopathogens that may be involved in the development of these floral abnormalities.

Therefore, this study aims to compare the spectrum and quantity of airborne bioparticles, such as *Ambrosia* pollen, fungal spores, and other microscopic propagules, above morphologically typical *Ambrosia* populations and those with reduced male flower production. Particular attention is given to the possible presence of airborne phytopathogens that could be linked to the observed floral malformations.

2 Materials and methods

2.1 Study area

The study was conducted in 2022 at six localities in Slovakia, Central Europe, including three sites with aberrant populations of *Ambrosia artemisiifolia* (Veľký Horeš – VH, Malá nad Hronom – MH, and Balvany – BV) and three sites with morphologically typical populations (Briežky – BR, Vrbová nad Váhom – VV, and Abov – AB) (Fig. 1, Table 1). All study sites were located in weedy agricultural fields with sandy-loam or loamy soils (Zaťko, 2002). The prevalent crop grown in these fields was sunflower.

Except for VH, which is located in the Východoslovenská nížina Lowland in the south-eastern part of the country, all other sites are situated in the Podunajská nížina Lowland in south-western Slovakia. In these lowland areas, *Ambrosia* is widely distributed (Hrabovský et al., 2024).

According to the Köppen-Geiger classification (Kottek et al., 2006), VH has a Dfb climate (snowy, fully humid, with warm summers), while the remaining study sites fall under the Cfb category, indicating a warm temperate, fully humid climate with warm summers.

In 2022, the mean annual temperature and total precipitation were 10.6°C and 526.2 mm at Košice, the nearest meteorological station to the VH site, and 11.9°C and 478.9 mm at Nitra, the nearest station to the other monitored sites (Slovak Hydrometeorological Institute).

Table 1
Overview of monitoring sites.

Monitoring site	Abbreviation	Coordinates	Elevation (m a.s.l.)
Veľký Horeš	VH	48.367222N, 21.876944E	99
Malá and Hronom	MH	47.856389N, 18.678889E	118
Balvany	BV	47.841389N, 18.003889E	110
Briežky	BR	47.822500N, 18.190833E	120
Vrbová nad Váhom	VV	47.821944N, 18.073611E	110
Abov	AB	47.878889N, 18.156667E	124

2.2 Definition of morphologically typical and aberrant populations of *Ambrosia*

Aberrant populations of *Ambrosia artemisiifolia* were identified at three sites in Slovakia. They showed a striking alteration in floral morphology (Fig. 2), with the key differences from morphologically typical plants summarised in Table 2.

2.3 Aerobiological sampling

Airborne bioparticles were collected on selected sampling days during the peak *Ambrosia* flowering season, defined as the period when the majority of individuals in the monitored populations were in full bloom. This ensured maximum bioparticle emissions and reliable comparisons between morphologically typical populations and those with reduced male flower production. Sampling was carried out exclusively on warm, sunny days without precipitation, with no rainfall occurring for at least two days prior to sampling. We also avoided days with strong wind conditions, which could have artificially influenced particle dispersion and concentration, potentially biasing the results. These criteria were set to ensure the most representative and stable atmospheric conditions for bioparticle collection.

Table 2
Morphological comparison between morphologically typical and aberrant plants of *Ambrosia artemisiifolia*

Feature	Morphologically typical plant	Aberrant plant
Determinate panicle	Corymbose	Racemose to corymbose
Determinate racemes	With staminate heads; ebracteate	Absent, or with pistillate heads only; bracteate or rarely ebracteate
Pistillate heads	In clusters along the lower part of the racemes or in the axils of upper leaves	In clusters or solitary in the racemes, may contain bisexual flowers
Staminate heads	Present in racemes	Absent or significantly reduced
Fruits	Fertile	Mostly sterile

Airborne bioparticles were collected using a portable personal volumetric Hirst-type sampler (Hirst, 1952) with an air flow rate of 10 L/min (<https://burkard.co.uk>), placed in a spot with abundant *Ambrosia* occurrence in the field borders. Sampling was conducted between 11:00 and 14:00, a time interval corresponding to the expected daily peak in airborne bioparticle concentrations. Bioparticles were captured on microscope slides coated with a silicone-based adhesive medium.

To account for vertical variability in airborne bioparticle distribution, sampling was conducted at three different heights: ground level (0 cm), 50 cm, and 150 cm above ground. Three independent 20-minute replicates were performed at each height to achieve a total exposure time of 60 minutes per height. This design minimised particle overlap on the adhesive surface, increased the resolution of captured diversity, and enabled a more comprehensive assessment of the airborne microbiome composition. Sampling at multiple heights was chosen because both the concentration and spectrum of airborne bioparticles were expected to differ with elevation above ground (Hugg et al., 2020; Charalampopoulos et al., 2022). The goal was to obtain as accurate a picture as possible of the local bioparticle environment immediately surrounding the analysed plant populations.

After exposure, microscopic slides were prepared by mounting them with glycerine jelly, stained with fuchsin. The samples were then analysed at 400× magnification under a light microscope (Motic B1-252SP) following standardised aerobiological procedures (Lacey and West, 2006). Pollen grains and fungal spores were identified using reference atlases (Grant Smith, 2000; Walter and Proctor, 2013; Li et al., 2023). Daily concentrations of individual bioparticles were expressed as pollen or spores per cubic meter of air.

Daily airborne *Ambrosia* pollen concentrations during the 2022 pollen season were obtained from the nearest permanent aerobiological monitoring stations (Košice – 48.72155N, 21.23887E for VH; Nitra – 48.30563N, 18.08382E for the remaining sites) using Hirst-type volumetric samplers (Burkard

Manufacturing Co. Ltd., UK). These data, sourced from the pollen database of the Public Health Authority of the Slovak Republic, were not included in statistical analyses but served to illustrate the regional aerobiological context during the sampling period. Based on these data, the *Ambrosia* main pollen season (MPS) was identified using the 90% method described by Nilsson and Persson (1981), which defines the beginning, end, and duration of the season. The season's intensity was assessed by calculating the seasonal pollen integral (SPIn, the cumulative sum of average daily pollen concentrations during the MPS) and by identifying the peak daily concentration.

2.4 Statistical analysis

To evaluate whether the composition of airborne bioparticles differed between sites with aberrant and morphologically typical populations of *Ambrosia* (hereinafter 'typical'), a permutational multivariate analysis of variance (PERMANOVA) was conducted using the *adonis2* function from the vegan package in R. For each site, the analysis was based on the average abundance values obtained from three different sampling heights. Prior to the analysis, taxon abundance data were standardised using the Hellinger transformation, which involves taking the square root of relative abundances. This transformation reduces the dominance of highly abundant taxa and enhances the suitability of the data for multivariate analyses based on Euclidean distances. The analysis was performed on a Bray–Curtis dissimilarity matrix derived from the standardised abundance data, comprising 57 taxa across six study sites.

3 Results

According to the data from the nearest permanent pollen monitoring stations (Košice for VH and Nitra for the remaining sites), the main pollen season (MPS) of *Ambrosia* began 8 days earlier and lasted 18 days longer in Nitra than in Košice in the analysed year. However, the overall intensity of the MPS, expressed as the seasonal pollen integral (SPIn) and peak daily values, was comparable between the two regions (Table S1). During the field sampling days (Table 3), *Ambrosia* pollen concentrations, based on the permanent monitoring station data, ranged from 12 to 86 pollen/m³ and average daily temperatures varied between 17.6 and 26°C.

Table 3

Mean daily airborne *Ambrosia* pollen concentration (PC) and temperature parameters from the nearest monitoring stations during field sampling. Site abbreviations are provided in Table 1.

Monitoring site	Monitoring day	PC (pollen/m ³)	T _{mean} (°C)	T _{max} (°C)	T _{min} (°C)
VH ^a	31 Aug	12	20.9	24.5	17.4
MH ^b	26 Aug	37	26.0	33.5	15.5
BV ^b	2 Sep	16	19.6	24.7	14.6
BR ^b	3 Sep	86	17.6	25.1	10.2
VV ^b	4 Sep	51	18.2	22.5	14.0
AB ^b	5 Sep	48	19.1	27.2	11.0
^a Data from the Košice aerobiological and meteorological stations; ^b Data from the Nitra aerobiological and meteorological stations; T_{mean} – mean daily air temperature; T_{max} – maximum daily air temperature; T_{min} – minimum daily air temperature					

The amount of airborne bioparticles recorded above aberrant and morphologically typical *Ambrosia* populations varied with the sampling height. In most cases, the highest concentrations of both *Ambrosia* pollen and fungal spores were detected at ground level, while the lowest values were observed at 150 cm above the ground (Table 4).

When considering the average values across all three sampling heights, *Ambrosia* pollen concentrations were 72.5% lower above sites with aberrant populations compared to those with typical populations. In contrast, the total concentrations of airborne fungal spores were similar above both population types (Table 4).

The concentrations and relative proportions of airborne fungal spores detected at the study sites with aberrant and typical *Ambrosia* populations are summarised in Table 5. In total, we recorded 51 fungal taxa, of which 40 were found above aberrant and 43 above typical populations. A total of 959 fungal spores/m³ were recorded above aberrant populations, compared to 1,027 spores/m³ above typical populations. The composition and relative abundance of fungal spore types differed between the two site types. In both environments, *Cladosporium* was the dominant taxon, accounting for 38.1% of spores above aberrant and 72.4% above typical populations. Several taxa were more abundant above aberrant populations, including *Alternaria* (21.3% vs. 13.5%), *Epicoccum* (13.6% vs. 1.3%), *Arthrinium* (5.0% vs. 0.2%), Uredinospores (7.7% vs. 1.1%), and *Torula* (1.88% vs. 0.19%). Conversely, some taxa were notably more abundant above typical populations, such as *Pithomyces* (3.9% vs. 1.6%), *Aspergillus/Penicillium* (0.2% vs. 1.0%), and *Stemphylium*, which was only detected at these sites (0.4%). Spore types exclusively recorded above aberrant populations included *Nigrospora*, *Cryptophyllachora*, and *Puccinia*, whereas *Stemphylium*, *Septoria*, *Fomes*, and *Fusicladium* were detected only above typical populations.

Table 4

Airborne *Ambrosia* pollen and total fungal spore concentrations at monitoring sites. Site abbreviations are provided in Table 1. Sampling heights are indicated in cm above the ground.

Monitoring site	Sampling height							
	0 cm		50 cm		150 cm		0-150 cm*	
	PC	SC	PC	SC	PC	SC	PC	SC
VH ^a	21	525	13	124	8	134	14	261
MH ^a	245	363	55	1,510	23	539	108	804
BV ^a	72	3,253	16	472	14	1,675	34	1,800
BR ^b	387	1,858	36	1,942	246	1,183	246	1,661
VV ^b	198	471	85	516	189	359	189	449
AB ^b	297	1,014	9	1,338	131	540	131	964
^a Site with aberrant <i>Ambrosia</i> population; ^b Site with morphologically typical <i>Ambrosia</i> population; PC – <i>Ambrosia</i> pollen concentration (pollen/m ³); SC – total fungal spore concentration (spores/m ³); *mean value								

PERMANOVA analysis showed that the two distinct *Ambrosia artemisiifolia* morphotypes explained 26.9% of the variance in the overall composition of airborne bioparticles ($R^2 = 0.2693$). However, this effect was not statistically significant ($F = 1.47$, $p > 0.05$; 719 unrestricted permutations). When considering only spores of phytopathogenic fungi infecting grasses and herbs, the morphotypes accounted for 22.4% of the variance ($R^2 = 0.2241$), yet this result was likewise not statistically significant ($F = 1.55$, $p > 0.05$; 719 permutations).

The log-transformed mean concentrations of airborne *Ambrosia* pollen and fungal spores of phytopathogenic taxa varied between the two morphotypes of *Ambrosia artemisiifolia* (Fig. 3). As expected, *Ambrosia* pollen was substantially more abundant above typical populations. In contrast, spores of several phytopathogenic fungi, such as *Epicoccum*, *Ustilago*, *Curvularia*, *Cryptophyllachora*, *Puccinia*, and *Alternaria*, reached higher concentrations above aberrant populations. Conversely, *Stemphylium*, *Cladosporium*, *Leptosphaeria* type, and

Table 5

Airborne fungal spore concentration and percentage contribution of all fungal spore types found in sites with aberrant and morphologically typical *Ambrosia* populations.

Spore type	TG	TM	Aberrant populations		Typical populations	
			SC (spores/m ³)	%	SC (spores/m ³)	%
<i>Agaricus</i> type	B	S	2	0.21	6	0.58
<i>Agrocybe</i>	B	S	0	< 0.01	1	0.1
<i>Albugo</i>	O	P	3	0.31	2	0.19
<i>Alternaria</i>	A	P/S	204	21.29	135	13.5
<i>Arthrinium</i>	A	S/P	48	5.01	2	0.19
<i>Ascobolus</i>	A	S	-	-	0	< 0.01
<i>Ascochyta</i>	A	P	0	< 0.01	1	0.1
<i>Aspergillus/Penicillium</i>	A	S/P	10	1.04	2	0.19
<i>Bipolaris</i>	A	P	14	1.46	11	1.07
<i>Botrytis</i>	A	P/S	-	-	0	< 0.01
<i>Bovista</i>	B	S	2	0.21	1	0.1
<i>Cercospora</i>	A	P	-	-	0	< 0.01
<i>Cerebella</i>	A	P	0	< 0.01	1	0.1
<i>Cladosporium</i>	A	S/P	365	38.1	744	72.44
<i>Coprinus squamatus</i>	B	S	1	0.1	1	0.1
<i>Coprinus</i> type	B	S	12	1.25	17	1.66
<i>Cryptophyllachora</i>	A	P	1	0.1	0	< 0.01
<i>Curvularia</i>	A	P	5	0.52	2	0.19
<i>Epicoccum</i>	A	S/P	130	13.57	13	1.27
<i>Exosporium</i>	A	S	6	0.67	-	-
<i>Fomes</i>	B	S/P	-	-	2	0.19
SC – total fungal spore concentration (spores/m ³) averaged across sites, rounded to the nearest whole number						
TG – taxonomic group (A – Ascomycota, B – Basidiomycota, M – Myxomycota, O – Oomycota)						
TM – trophic mode (S – saprotroph, P – plant pathogen)						

Spore type	TG	TM	Aberrant populations		Typical populations	
			SC (spores/m ³)	%	SC (spores/m ³)	%
<i>Fusarium</i>	A	P/S	-	-	0	< 0.01
<i>Fusicladium</i>	A	P	-	-	1	0.1
<i>Ganoderma</i>	B	S/P	3	0.31	6	0.58
<i>Leptosphaeria</i> type	A	P/S	2	0.21	3	0.29
<i>Leveillula taurica</i>	A	P	1	0.1	2	0.19
<i>Melanospora</i>	A	S	0	< 0.01	-	-
<i>Metasphaeria</i>	A	S/P	0	< 0.01	-	-
Myxomycetes	M	S	4	0.42	7	0.68
<i>Neohendersonia</i>	A	P/S	-	-	-	-
<i>Nigrospora</i>	A	S/P	1	0.1	-	-
<i>Oidium</i> type	A	P	2	0.21	1	0.1
<i>Panaeolus</i>	B	S	-	-	1	0.1
<i>Periconia</i>	A	S/P	1	0.1	1	0.1
<i>Peronospora</i>	O	P	1	0.1	1	0.1
<i>Pithomyces</i>	A	S/P	15	1.57	40	3.89
<i>Pleospora</i>	A	S/P	2	0.21	1	0.1
<i>Polythrincium</i>	A	S/P	0	< 0.01	0	< 0.01
<i>Puccinia</i>	B	P	2	0.21	-	-
<i>Sclerotinia</i>	A	P	0	< 0.01	-	-
<i>Septoria</i>	A	P	-	-	1	0.1
<i>Sordaria</i>	A	S	0	< 0.01	0	< 0.01
<i>Spegazzinia</i>	A	S	0	< 0.01	0	< 0.01
SC – total fungal spore concentration (spores/m ³) averaged across sites, rounded to the nearest whole number						
TG – taxonomic group (A – Ascomycota, B – Basidiomycota, M – Myxomycota, O – Oomycota)						
TM – trophic mode (S – saprotroph, P – plant pathogen)						

Spore type	TG	TM	Aberrant populations		Typical populations	
			SC (spores/m ³)	%	SC (spores/m ³)	%
<i>Sporormiella</i>	A	S	-	-	0	< 0.01
<i>Stemphylium</i>	A	P	0	< 0.01	4	0.39
<i>Tilletia</i>	B	P	0	< 0.01	-	-
<i>Torula</i>	A	S/P	18	1.88	2	0.19
Uredinospores	B	P	74	7.72	11	1.07
<i>Urocystis</i>	B	P	-	-	0	< 0.01
<i>Ustilago</i>	B	P	25	2.61	3	0.29
Xylariaceae	A	S	5	0.52	1	0.1
Total			959	100	1,027	100
SC – total fungal spore concentration (spores/m ³) averaged across sites, rounded to the nearest whole number						
TG – taxonomic group (A – Ascomycota, B – Basidiomycota, M – Myxomycota, O – Oomycota)						
TM – trophic mode (S – saprotroph, P – plant pathogen)						

Ascochyta were more abundant above typical populations. These differences suggest potential changes in the airborne fungal community structure associated with reduced male flower production in aberrant populations.

4 Discussion

The notable differences in pollen production between aberrant and typical populations can be explained by a higher proportion of female flowers, although some phenotypes may contain bisexual flowers with functional stamens. Even within sites dominated by aberrant *Ambrosia* morphotypes, airborne pollen concentrations showed notable variation (14–108 pollen/m³). This variability may reflect differences in plant stature and site-specific conditions. According to Lommen et al. (2018), taller *Ambrosia* individuals produce more pollen, and plant height is influenced by soil type, aeration, and microclimatic factors. On recently disturbed soils with low sand content and under warm and moist conditions, *Ambrosia* tends to grow taller and denser, leading to higher pollen output. For example, at the MH site, the tallest and densest stands of *Ambrosia* corresponded with the highest measured pollen concentrations. In contrast, the VH site, where *Ambrosia* grew on compacted, untilled fallow soil, had sparse vegetation and the lowest pollen levels among aberrant sites, possibly due to lower nutrient content levels compared to arable land (Fumanal et al., 2007; Lommen et al., 2018). Similar patterns were observed among typical

populations, where pollen concentrations ranged from 131 to 246 pollen/m³. The lowest levels were detected in AB, characterised by sandy soil and shorter *Ambrosia* plants with lower abundance. These data highlight the importance of site conditions in shaping airborne pollen loads, even within morphologically uniform populations.

In addition to factors such as source organism abundance and meteorological conditions, the concentration of airborne bioparticles can also be influenced by sampling height (Després et al., 2012; Xiao et al., 2013; Rojo et al., 2019; Núñez and Moreno et al., 2020). This is because the altitude that bioaerosols can reach depends largely on their aerodynamic properties, which are, in turn, governed by their physical and chemical characteristics (Chakraborty et al., 2001; Smith et al., 2011). Sánchez-Parra et al. (2021) observed that larger particles, such as pollen grains, tend to settle at lower altitudes due to their limited buoyancy. In contrast, bacteria and small fungal propagules are more frequently detected at higher elevations owing to their greater dispersal potential. Moreover, to capture particles originating from a broader area, sampling should be conducted at higher elevations (typically 10–20 m above ground level), where the air is more thoroughly mixed (Lacey and West, 2006). Conversely, if the objective is to sample local bioparticles, lower sampling heights, ideally below 150 cm, are recommended (Rojo et al., 2019). Previous studies have shown that the concentration of locally sourced particles tends to decrease with increasing sampling height, due to the dilution effect (Rojo et al., 2020), a trend also evident in our research. This effect may be particularly pronounced for fungal spores with protective outer layers contributing to their weight and increasing settling velocities (Després et al., 2012). From this perspective, placing samplers closer to the ground may be optimal for capturing such particles. However, this height is also more susceptible to resuspension of particles from the soil surface, possibly transported there by wind from a broader area, especially under windy conditions. Due to microscale environmental dynamics, fluctuations at this height are also more pronounced (Rojo et al., 2019). To better capture the vertical variability and assess atmospheric heterogeneity in the near-surface layer, we employed a multi-level sampling strategy, placing samplers at 0 cm, 50 cm, and 150 cm above ground. The height of 1.5 m above ground is frequently employed in aerobiological sampling related to respiratory allergies, as it closely approximates the human breathing zone, a standard established to better represent human exposure (Hugg et al., 2020). By averaging measurements obtained at three heights, our approach aimed to yield a more representative estimate of airborne bioparticle concentration above the studied *Ambrosia* populations.

Biotrophic fungal pathogens, especially rust fungi, have proven to be effective classical biological control agents (BCA) due to their high host specificity and potential to cause severe epidemics in invasive plant populations (Evans, 2013). They often do not result in rapid tissue death in their host plants and may not be lethal at all (Spanu, 2012; Kemen et al., 2015; Schäfer et al., 2010; Perlin et al., 2015), but can significantly impact host fitness by suppressing pollen production (Schäfer et al., 2010; Perlin et al., 2015), increasing seedling mortality (Marçais and Desprez-Loustau, 2014), limiting growth in mature individuals (Bert et al., 2016), or contributing to population decline and fragmentation (Jousimo et al., 2014).

Many of the approximately 20 fungal pathogens identified in association with *Ambrosia* species across Eurasia tend to have broad host ranges and generally exert only minimal effects on the plant under natural field conditions (Kiss et al., 2003). In our study, increased concentrations of the spores of the following phytopathogenic fungal genera associated with *Ambrosia* were recorded above aberrant populations, compared to typical ones: *Albugo*, *Alternaria*, *Cryptophyllachora*, *Fusarium* and *Sclerotinia*. Higher concentrations of *Bipolaris*, *Cercospora*, *Curvularia*, *Epicoccum*, *Puccinia*, and *Ustilago* were also recorded.

The presence of *Cryptophyllachora* spores in particular deserves attention. This genus includes *C. eurasiatica* L. Kiss, Kovács & R.G. Shivas, an unculturable fungus that has previously caused destructive outbreaks on *A. artemisiifolia* in Hungary and Ukraine, affecting stems, leaves, and inflorescences (Vajna et al., 2000; Hayova, 2006; Kiss et al., 2018). Despite the absence of visible disease symptoms (irregular brown lesions with yellow halos and black perithecia on the upper leaf surface) on the examined plants in our study sites, spores of this genus were consistently detected, with higher concentrations above aberrant populations suggesting possible asymptomatic infection or early-stage colonisation. Such latent or subclinical infections may still impact host physiology and reproductive capacity.

The genus *Albugo* contains *A. tragopogonis* (Pers.) S. F. Gray (white rust), another known pathogen of *Ambrosia*, which has been reported to suppress pollen and seed production (Hartmann and Watson, 1980). This disease typically manifests as white pustules on leaves, which were not observed in our study. Since, according to the mentioned study, symptomless individuals may still produce normal amounts of pollen, we can rule it out as an unlikely cause of the aberrant morphotype.

The genus *Sclerotinia* includes a well-documented ragweed pathogen in both North America (Farr et al., 1989; Boland and Hall, 1994) and Europe, *S. sclerotiorum* (Lib.) de Bary. Its first European record was in Hungary in the late 1990s, where infected plants with wilting, stem lesions, and black sclerotia were found mainly near heavily infested sunflower fields (Bohár and Kiss, 1999). While we did not observe symptomatic individuals or sclerotia, its spores were more abundant above populations with altered reproductive traits, possibly reflecting early, undetectable stages of infection or proximity to infected host material in nearby environments.

The genus *Alternaria*, frequently isolated from ragweed surfaces, including inflorescences, is known to colonise pollen grains (Tóth et al., 2009; Magyar et al., 2022). While *Alternaria* is generally not associated with macroscopic damage to reproductive structures, its presence on and around inflorescences may interfere with pollen development or viability. In this context, increased airborne spore loads above aberrant populations could indicate intensified interactions between fungi and floral tissues.

Although not associated with floral morphology, *Fusarium* species are commonly linked to root infections in *A. artemisiifolia*, leading to altered plant growth and vitality (Li and Li, 1993). In our study, however, *Fusarium* is unlikely to explain the lack of male flowers, as these symptoms are typically linked to above-ground tissues and reproductive development.

Finally, although no macroscopic signs of *Puccinia xanthii* Schwein. infection were observed, the elevated concentration of *Puccinia* spores above aberrant populations suggests its potential presence in early or latent stages. *P. xanthii*, a rust fungus previously reported on *Ambrosia*, is capable of systemically infecting its host and may interfere with flower development or fertility, particularly in male inflorescences (Kiss et al., 2003; Ellison et al., 2008). While it was initially selected as a BCA candidate, recent studies suggest its limited occurrence on *A. artemisiifolia* in Europe, with confirmed records only from related *Xanthium* L. species (Dávied et al., 2003).

Overall, the elevated spore concentrations of several phytopathogenic fungi above aberrant populations of *A. artemisiifolia* suggest potential links between airborne pathogen pressure and changes in reproductive morphology. While visible disease symptoms were largely absent, these findings raise the possibility of cryptic fungal infections, particularly by taxa such as *Cryptophyllachora*, *Albugo*, or *Puccinia*, contributing to the observed deviations from typical floral development. Further targeted investigations combining histopathological and molecular approaches will be necessary to confirm these associations and clarify causal relationships.

Although the PERMANOVA did not yield statistically significant results, the relatively high proportion of explained variance ($R^2 = 0.2693$) indicates a potentially biologically meaningful differentiation in the taxonomic composition of airborne fungal spore types between sites with distinct *Ambrosia* morphotypes. The absence of statistical significance is likely attributable to the limited number of sampling sites ($n = 3$ per group), which inherently reduces the statistical power to detect subtle ecological patterns. These results could become significant with increased sample size, more controlled environmental replication, or additional years of data collection.

5 Conclusions

Aberrations in inflorescence development of *Ambrosia artemisiifolia* populations can have several causes, including genetic mutations, environmental stress or pathogen-induced hormonal imbalances. Our study reveals that aberrant populations of this invasive species in central Europe are associated with differences in the surrounding aerobiome compared to populations with standard morphology. Lower concentrations of *Ambrosia* pollen detected above aberrant populations can be explained by the lower ratio of stamen-bearing flowers. The elevated levels of certain phytopathogenic fungal spores, including *Cryptophyllachora*, *Albugo*, and *Puccinia*, suggest a potential link between airborne pathogen pressure and the observed floral abnormalities, possibly indicating the presence of cryptic fungal infections affecting reproductive development. Future work incorporating targeted histopathological assessments and molecular diagnostics will be essential to verify pathogen involvement and to disentangle the complex interactions between host physiology and environmental microbial pressures. Ultimately, understanding these relationships may contribute to more effective management strategies for invasive *A. artemisiifolia* populations and provide broader insights into plant adaptation and pathogen-mediated evolution in novel ecosystems.

Declarations

Conflict of interest

The authors declare that they have no known financial interests or personal relationships that might influence the work reported here.

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Author Contribution

J.Š. conceptualised the study, developed the methodology, supervised the research, performed validation and visualisation, and wrote the original draft. M.Ž. analysed the data and contributed to reviewing and editing the manuscript. P.T. curated the data and contributed to reviewing and editing the manuscript. E.Z. contributed to the visualisation and to reviewing and editing the manuscript. M.H. analysed the data, contributed to the visualisation, and contributed to reviewing and editing the manuscript.

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Data availability statement

The datasets generated and/or analysed during the current study are available from the corresponding author upon reasonable request.

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Figures

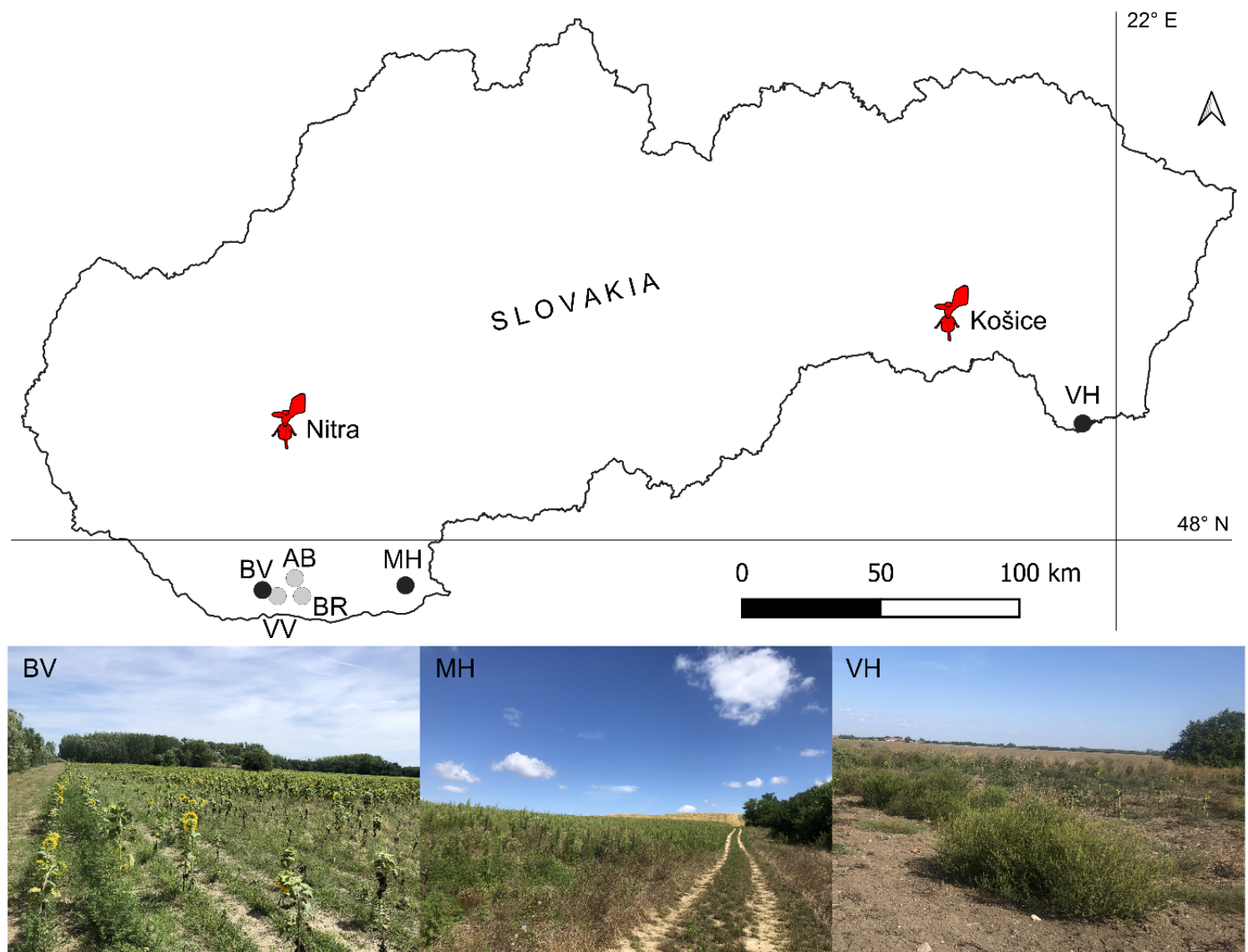


Figure 1

Locations of study sites with morphologically typical (grey dots) or aberrant *Ambrosia* plants (black dots), equipped with portable air samplers, and the nearest permanent aerobiological monitoring stations (red symbols). Abbreviations of study sites are provided in Table 1 (photos: Peter Tóth).



Figure 2

Aberrant *Ambrosia artemisiifolia* plant: A) young plant; B) mature plant with a panicle of mature achenes (photos: Peter Tóth)

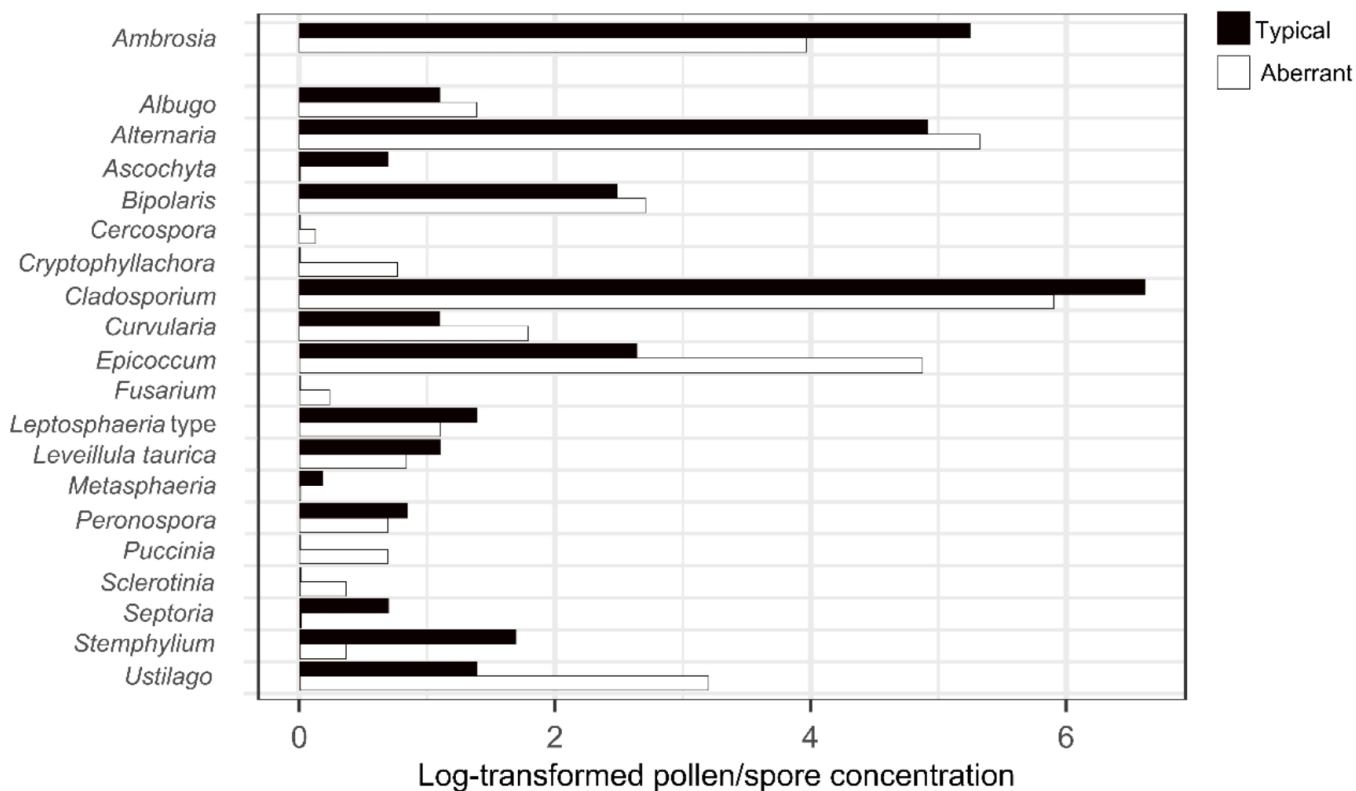


Figure 3

Log-transformed mean concentrations of airborne *Ambrosia* pollen and fungal spores of phytopathogenic fungi infecting grasses and herbs recorded above morphologically typical (black bars) and aberrant (white bars) populations of *Ambrosia artemisiifolia*. The figure includes only fungal taxa whose average concentration across the three analysed sites with either aberrant or morphologically typical *Ambrosia* populations reached ≥ 1 spore/m³.

Supplementary Files

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