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Review

Isolating the species element in grass pollen allergy: A review

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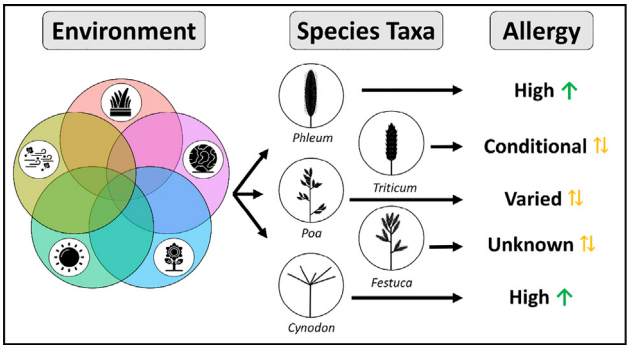
HIGHLIGHTS

- Grass species and their associated allergens vary widely in allergenic potential.
- Temperate and subtropical grass species should be considered separately.
- Allergen homology should be investigated together with species taxonomy.
- eDNA and molecular ecological methods can connect the biosphere and the atmosphere.

GRAPHICAL ABSTRACT



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ABSTRACT

Grass pollen is a leading cause of allergy in many countries, particularly Europe. Although many elements of grass pollen production and dispersal are quite well researched, gaps still remain around the grass species that are predominant in the air and which of those are most likely to trigger allergy. In this comprehensive review we isolate the species aspect in grass pollen allergy by exploring the interdisciplinary interdependencies between plant ecology, public health, aerobiology, reproductive phenology and molecular ecology. We further identify current research gaps and provide open ended questions and recommendations for future research in an effort to focus the research community to develop novel strategies to combat grass pollen allergy. We emphasise the role of separating temperate and subtropical grasses, identified through divergence in evolutionary history, climate adaptations and flowering times. However, allergen cross-reactivity and the degree of IgE connectivity in sufferers between the two groups remains an area of active research. The importance of future research to identify allergen homology through biomolecular similarity and the connection to species taxonomy and practical implications of this to allergenicity is further emphasised. We also discuss the relevance of eDNA and molecular ecological techniques (DNA metabarcoding, qPCR and ELISA) as important tools in quantifying the connection between the biosphere with the atmosphere. By gaining more understanding of the connection between species-specific atmospheric eDNA and flowering phenology we will further elucidate the importance of species in releasing grass pollen and allergens to the atmosphere and their individual role in grass pollen allergy.

Contents

1. Introduction 2
2. Biogeography and ecology 2

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3. Health and immunology . . . 4
3.1. Grass pollen allergy . . . 4
3.2. Allergens and grass species . . . 4
4. Aerobiology . . . 5
4.1. Pollen monitoring . . . 5
4.2. Pollen morphology . . . 6
4.3. Pollen production . . . 6
5. Flowering phenology . . . 7
5.1. Phenological classification . . . 7
5.2. Population dynamics . . . 7
5.3. Seasonal sequential flowering . . . 8
5.4. Release and dispersion processes . . . 9
6. Molecular identification . . . 9
7. Conclusions and recommendations for future research . . . 10
CRediT authorship contribution statement . . . 10
Data availability . . . 10
Declaration of competing interest . . . 10
Acknowledgements . . . 10
References . . . 10

1. Introduction

Grasses (Poaceae) are a near ubiquitous family of plants that dominate and define many ecosystems, being one of the few plant families found on all continents (Linder et al., 2018; Peterson and Soreng, 2022). Grasses are keystone species in many biomes, being the primary food-source for many species that in-turn reinforce the grass dominance in the landscape (Blair et al., 2014). Grasses are also fundamentally important for humans, being arguably the evolutionary driving force for human culture and society through agriculture (Currie et al., 2015; DeWet, 1981) and providing many critical ecosystem services (Bengtsson et al., 2019). In most cultures grasses directly or indirectly provide 40 % of the human nutritional requirement, primarily in the form of corn (*Zea mays*), rice (*Oryza sativa*) and wheat (*Triticum aestivum*), making them the most important food source for humans (van Wyk, 2019). Furthermore, grasses provide a basic necessity to domesticated animals through grazing, hay and silage (Rose, 1989).

Grasses provide humanity with a plethora of benefits but there are also downsides, primarily mediated through allergy (García-Mozo, 2017). About 40 % of the adult European population experiences some type of pollen allergy, with the majority being grass pollen (D'Amato et al., 2007). This contributes to substantial negative effects for public health and societal productivity (Crystal-Peters et al., 2000). However, not all grass species provoke the same response in the sufferer (Luo et al., 2016), likely due to species-specific conditions that comes down to biological, ecological and genetic factors (Cresti and Linskens, 2000; Jung et al., 2021). Therefore, identifying whether some grasses are of higher allergenic relevance is critical in mitigating societal and medicinal costs. Research into how grass pollen varies in the atmosphere (Calderon-Ezquerro et al., 2018; García-Mozo et al., 2010a), which species are most allergenic to the human population (Pablos et al., 2016) and the spatiotemporal flowering of grasses (Ghitarrini et al., 2017a) have increased understanding of the relationship between grasses and allergy, but the picture is incomplete.

Due to the homogeneous nature of grass pollen morphology, a great deal of uncertainty exists in classifying and quantifying the pollen of different species of Poaceae present in the air (Morgado et al., 2015). However, newly developed molecular techniques and innovative ways of connecting aerobiology with ecology (Campbell et al., 2023; Oteros et al., 2020; Rojo et al., 2022; van Hout et al., 2008) are increasing our understanding of the link between the biosphere and the atmosphere. This is an interdisciplinary topic. This review therefore aims to summarize and synthesize the current knowledge of the species element in grass pollen allergy (Fig. 1), as well as highlight key questions and make recommendations for future research.

2. Biogeography and ecology

It is estimated that there are around eleven thousand Poaceae species with circumglobal distribution, making it the fifth largest plant family (Bouchenak-Khelladi et al., 2010). Global species richness varies depending on large-scale habitat heterogeneity and distance to the poles, with subtropical latitudes being more likely to host assemblages of greater species diversity (Fig. 2). Species richness and distribution also varies between genera, as genera vary in the continental region hosting their respective highest species diversity (Table 1). The ten most species rich genera comprise 32.8 % of all the extant species while simultaneously 34.2 % of the 713 extant genera being monotypic, consisting of only one recognized species (Clayton et al., 2002). *Festuca* is the grass genus in Europe with the highest species richness, while in South America it is *Paspalum* and in Africa *Eragrostis*. This has led to the distinction and classification of temperate and subtropical grass genera, although many genera have species on multiple continents and latitudes based on evolution and biogeography (Bryceson and Morgan, 2022; Gallaher et al., 2022).

The classification of temperate and subtropical grasses is partly phylogenetic in origin, due to many temperate grasses belonging to the BOP-clade while many subtropical grasses belong to the PACMAD-clade (Soreng et al., 2022, 2017). The biogeography and evolutionary processes have created distinct species with specific habitat requirements, often making individual species ranges restricted even though the genus itself is not (Bock and Bock, 1986; Cope and Gray, 2009). Distinct species ranges in relation to large biogeographical patterns and processes give rise to biomes, with multiple biomes being classified as grasslands due to the dominance of grasses (Strömberg, 2011). Examples of grassland biomes include the Pampas of Southern America, the Prairies of Northern America and the Steppes in Temperate Asia. Grass-dominated systems also exist on smaller scales, created by local circumstances in meteorology, geography and soil, e.g., calcareous grasslands or coastal salt marshes, each with unique species adapted to the specific conditions in these habitats (Baba, 2004; Penk et al., 2020). Furthermore, anthropogenic activity has been suggested as a factor contributing to the expansion of grassland systems, primarily through fire and grazing dynamics (Behling et al., 2007; Bliege Bird et al., 2008; Vorontsova et al., 2016).

Species can be further characterized based on life strategies tied to their ecology. One such evolutionary strategy is the photosynthetic carbon fixating pathway, either C3 or C4 (Pau et al., 2013). C3-species are classified as cool season grasses while C4-species are classified as warm season grasses. C4-species dominate the tropics due to their ability to survive and photosynthesize more effectively in warmer and dryer climates while C3-grasses dominate elsewhere (Edwards and Still, 2008; Taylor et al., 2010). While the PACMAD-clade contains both C3- and C4-grasses, the BOP-clade contains only C3 (Hodkinson, 2018).

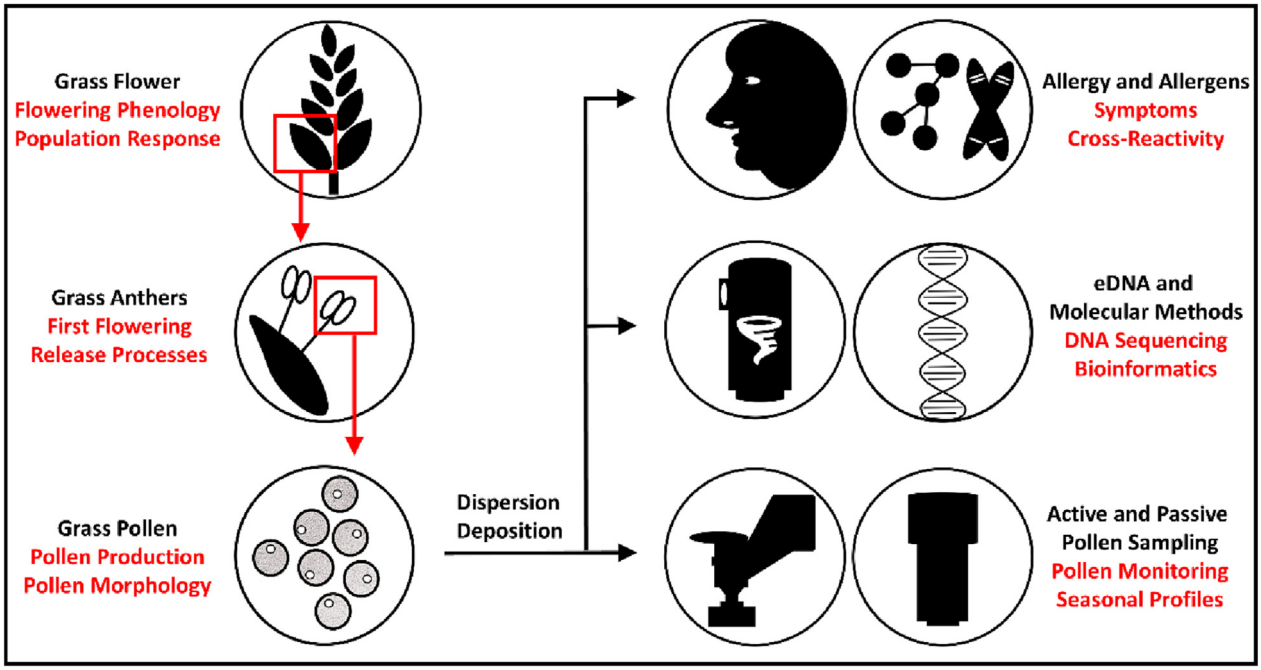

Fig. 1. Schematic drawing of the aerobiological process from source to sink regarding grass pollen and grass pollen allergy.

Another strategy is the duration of the life cycle, with grasses being either annuals or perennials (Garnier, 1992). Annuals complete the life cycle within one year while perennials complete it in multiple years, with 82 % of grass species being considered perennials (Clayton et al., 2002). The lifespan of a species will have vital implications to its phenology and ecology since perennials are able to survive several seasons while annuals cannot (Ergon, 2017). Perennials can therefore accumulate resources between seasons, produce additional side-shoots and colonize larger areas than annuals, all features that will increase their survivability (Friedman and Rubin, 2015). However, annuals have higher growth rates and would be the favoured life-strategy in unpredictable environments (Garnier, 1992). Special conditions apply to species considered cereals and grown in the agricultural setting, due to their requirements being artificially maintained (Qi et al., 2018), although their growth and survivability is restricted to some extent by external meteorological and climatological conditions as well (Bos and Neuteboom, 1998; Lecerf et al., 2019; van der Velde et al., 2018).

In general, the presence and abundance of a species on a local scale will not only be determined by habitat requirements and life strategies but also land-use and management (Jung et al., 2022; Theuerkauf et al., 2015). Land-use will dictate the extent of the area that can be colonized by plants (Gerstner et al., 2014; Maurer et al., 2006; Picornell et al., 2023). The abundance of grasses is expected to be low in the concrete landscape of urban areas, as only the hardiest species will be able to survive in the limited soil and cracked concrete. However, suitable habitats exist in the urban matrix to some extent, such as verges and parks, that will be expected to contain multiple species (Hruška, 2000). The dominance of grasses is expected to increase in areas with increased soil content and openness, and the absence of other vegetation. Maximum abundance is reached in grass dominated land-types such as pastures, meadows, grasslands and some agricultural areas (McInnes et al., 2017).

While land-use is relevant in providing the space for plants to establish, management will determine if plants can flourish (Skjøth et al., 2013). If all plants in an area are kept from flowering, either by mowing, cutting,

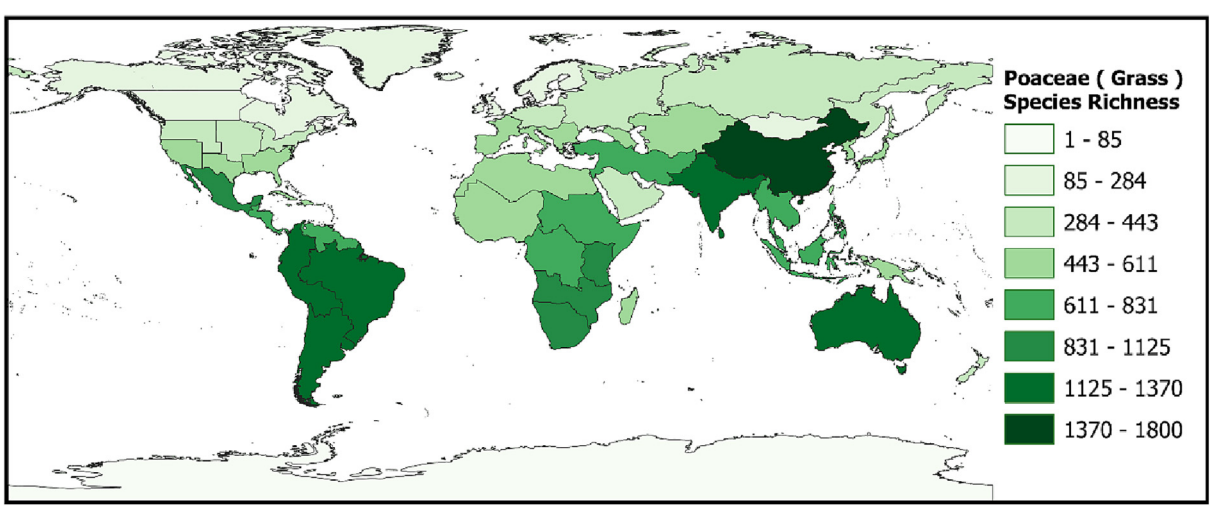

Fig. 2. Global Poaceae species richness following The Online World Grass Flora (GrassBase) organized by Kew Royal Botanical Gardens and categorized using level 2 of the World Geographical Scheme for Recording Plant Distributions (WGSRPD).

Table 1
Continental species distribution of the ten most species rich Poaceae genera. The taxonomy follows the Online World Grass Flora (GrassBase) organized by Kew Royal Botanical Gardens. The geography is based on level 1 of the World Geographical Scheme for Recording Plant Distributions (WGSRPD). The total Poaceae species richness per continental region can be found at the bottom.

Taxa	Continental species distribution									Total
Genus	Europe	Africa	Asia Temperate	Asia Tropical	Australasia	Pacific	America Northern	America Southern	Antarctic	Species
Festuca	192	67	158	49	19	8	62	163	5	621
Poa	54	29	158	96	84	7	80	120	10	496
Panicum	6	175	27	42	40	26	108	198	0	463
Eragrostis	10	212	51	56	75	33	53	91	0	401
Stipa	47	20	133	30	67	1	38	76	0	348
Paspalum	4	11	17	14	19	15	96	290	1	326
Aristida	1	70	23	25	59	5	50	100	0	284
Calamagrostis	15	2	80	31	40	2	38	99	1	266
Digitaria	4	112	31	56	47	21	37	81	1	263
Elymus	25	9	173	30	15	1	41	10	2	241
Sum (#)	358	707	851	429	465	119	603	1228	20	3709
Total (#)	945	2595	2991	2187	1566	437	1779	3257	85	11,313
Sum (%)	37.88 %	27.24 %	28.45 %	19.62 %	29.69 %	27.23 %	33.90 %	37.70 %	23.53 %	32.79 %

grazing or removal of plant material, the pollen contribution will be eliminated, even if the area is technically covered by productive grass species (Emberlin et al., 1993; Jetschni and Jochner-Oette, 2021). Although grasses are physiologically adapted to grazing, management will have a fundamental role in their ability to reach flowering potential (Brock et al., 1996; Wang et al., 2018). Management is expected to be especially relevant in pastures and meadows, areas that depending on the presence and placement of animals can be fully grazed, or fully grown (Smith et al., 2000). Ultimately, the species distribution and their ability to survive and flower will dictate the likelihood of pollen exposure, and thereby allergy of nearby sufferers.

3. Health and immunology

3.1. Grass pollen allergy

Pollen allergy affects 10–20 % of the global human population while being more common in Europe (Akdis and Agache, 2014; D'Amato et al., 2007). Grass, followed by birch (*Betula*) and ragweed (*Ambrosia*), are the leading pollen allergies globally (Akdis and Agache, 2014; Newson et al., 2014). The effects normally include sneezing, increased nasal secretions and itching in the nose and eyes, but can also indirectly include fatigue, lack of sleep, headaches and a general discomfort brought on by the direct effects (Greiner et al., 2011; Wallace et al., 2008). Pollen can also contribute to atopic asthma, having been referred to as 'one airway, one disease' (Bachert et al., 2004). Allergic rhinitis is not only physically debilitating but it also contributes to a loss in quality of life (Šaulienė et al., 2016) and a measurable loss of productivity for the entire society (Crystal-Peters et al., 2000; Lamb et al., 2006). Interactions between air pollution and allergy further complicates the issues (Sénéchal et al., 2015), as air pollution has been found to exacerbate asthma (Osborne et al., 2017) and contribute to modulation of the allergenic activity and immunological responses of pollen allergens (D'Amato et al., 2010; Fernández-González et al., 2023; Rogerieux et al., 2007). Grass pollen has traditionally been treated monolithically in the context of equal allergenicity (Hyde, 1973, 1972; Solomon, 1984). This has been questioned in the last few decades due to differential biochemical composition between species (Suphioglu and Mansur, 2000) and an observable difference in immunological reactivity between species pollen in sufferers (Erkara et al., 2009; Park et al., 2012).

3.2. Allergens and grass species

Evolutionary adaptation and biochemical differentiation of each grass species creates a range of different chemical variants of the same functional product seen in proteins, lipids and other components on and in the grass pollen grain (Devis et al., 2017). By classifying and quantifying specific proteins and lipids into categories and subsequently identifying how they affect the pollen sufferer, individually and in combination with other components, it is theoretically possible to determine the allergenicity of each species (Davies, 2014). Each identified allergenic component is then effectively categorized as an allergen and further classified based on the genus and species it was isolated from and to the group of allergens based on the biochemical functionality (Chen et al., 2016; Knox and Suphioglu, 1996). Grass pollen allergens are classified into 13 allergen groups, with each group containing allergens isolated from different model species, e.g. group 5 containing the allergen Phl p5, isolated from *Phleum pratense*, and Lol p5 isolated from *Lolium perenne*. Allergen groups vary in potency, with groups 1 and 5 having been shown to provoke allergenic responses the strongest, affecting 65–90 % of sufferers (Andersson and Lidholm, 2003; Hrabina et al., 2008a).

Allergens from different species share commonality between and within allergen groups based on amino-acid sequence, functionality of the compound and common evolutionary ancestry. This contributes to the cross-reactivity between species seen in many grass pollen sufferers (Aleksic et al., 2014; Leiferman and Gleich, 1976; Mohapatra et al., 2005; Pomés et al., 2018; Radauer et al., 2014; Van Ree et al., 1992). However, the cross-reactivity will be expressed unpredictably due to species diversity and distribution (Aud-In et al., 2019). An immune-system primary allergenic response from allergens of one dominant species can be strengthened via cross-reactivity from another species flowering at the same time, or perhaps earlier in the season (D'Amato et al., 1998). This does not necessarily mean that higher species richness is contributing to a stronger allergenic response, more airborne allergens or an increased chance of cross-reactivity, but this has not yet been fully explored.

It is also unknown to what extent species within the same taxonomic group share allergen homology and to what extent this plays a part in terms of pollen allergy. Allergen homology here refers to the degree of biomolecular similarity between allergens within the same group (e.g., Phl p1 and Lol p1 or Phl p5 and Cyn d5) (Aud-In et al., 2019) and if the allergen Lol p1 is the exact same between the species *L. perenne* and *L. multiflorum*, or if they are variants, and to what degree this influences immunological interactions (Devis et al., 2017). One of the main reasons for this inconsistency and uncertainty is the isolation of allergens from only model species, e.g., Phl p5 from *P. pratense* (and no other *Phleum* species) and Lol p1 from *L. perenne* (and no other *Lolium* species). It is possible that all species within a genus are equally allergenic due to containing the same allergens, or that other evolutionary, ecological or biological factors on a species level determines the presence/absence and abundance of allergens. These uncertainties have made it difficult to ascertain which species the sufferer is primarily sensitive towards without extensive immunological investigation, although evidence suggests that cross-reactivity between species, e.g., *Festuca* and *Lolium*, is less than previously thought (Harding et al.,

2021). Due to the inherent complexity of conducting experiments using combinations of allergens on live subjects the general allergenicity has not been established for all species, but the research has shown that some species, or at least some genera, are more allergenic than others (Abreu et al., 2008).

Multiple allergenic indexes have been developed from combining plant life strategy traits and limited studies on allergenic compounds (Cariñanos et al., 2014; Hruška, 2003; Suanno et al., 2021b). These studies have suggested life strategy traits associated with high allergenicity include plants that are tall, perennial, with good abundance, the ability to produce relatively high amounts of pollen and to have long flowering periods. Grasses that fit this description include, e.g., species in the temperate genera *Anthoxanthum*, *Dactylis*, *Holcus*, *Lolium*, *Phleum* and *Poa* and the subtropical genera *Cynodon* and *Paspalum*. Species from these genera have also been shown in clinical trials to be highly allergenic, e.g., perennial ryegrass (*Lolium perenne*) (Hew et al., 2020), Timothy (*Phleum pratense*) (Rossi et al., 2001), Bermuda grass (*Cynodon dactylon*) (Liao et al., 2020) and bahai grass (*Paspalum notatum*) (Davies et al., 2005). *Phleum pratense* is the grass species that has been investigated to the largest extent in terms of allergenic compounds and its health effects (Almeida et al., 2019; Araujo et al., 2016; Tripodi et al., 2012; Westritschnig et al., 2008), having allergens isolated from at least 11 allergen groups. A few studies have compared the immunological responses of multiple species allergens on the same study participants and found differences in IgE-responses between the allergens of temperate and subtropical grasses, even when accounting for the same allergen-group (Davies et al., 2011; Kailaivasan et al., 2020). This suggests inherent differences between the allergens, or a consequence of exposure to locally predominant species. The Melbourne thunderstorm asthma event of 2016 illustrates these varying allergenic responses, since individuals of Asian and Indian ethnicity were far more prone to severe symptoms than those of other ethnicities (Thien et al., 2018). This event was further linked to *Lolium* allergens, primarily Lol p1 and Lol p5 (Hew et al., 2020). This contrasts with homogeneous immunological responses to a few select *Phleum* allergens that have been found to permeate multiple human populations on an international scale when identifying grass pollen allergy (Laffer et al., 1996).

Festuca is the most species rich grass genera, but a limited number of studies have been conducted to explore the allergenicity of its species (Harding et al., 2021). The richness makes the genus an ideal candidate to investigate the association between biogeography and allergen homology. Furthermore, it is possible that some allergenic species lack studies due to few grass allergy symptoms being reported, which is possibly the case with the genera *Molinia* and *Phragmites*, both belonging to the PACMAD-clade (Soreng et al., 2017). In Northern Europe these genera flower during the end of the season, when pollen concentrations tend to be low (Bastl et al., 2020; Buters et al., 2015), likely leading to their allergenicity being under-investigated in temperate regions (Davies, 2014; Nony et al., 2015). The exception to under-investigated taxa is pollen from cereal grasses (e.g., *Avena sativa* (oats) and *Hordeum vulgare* (barley)), that despite their high allergenicity (Hrabina et al., 2008b) do not disperse far due to their large and heavy pollen (Jarosz et al., 2003). This makes their allergenic contribution strong on a localized scale surrounding agricultural areas, but weak otherwise (Damialis and Konstantinou, 2011).

The main method for investigating potential sensitivity of an individual to grass pollen is by using the Skin Prick Test (SPT) (Heinzerling et al., 2013). This method involves pricking the skin with a purified allergen or a cocktail of different allergens from a species or group of species, compared with a standardized dose of histamine (Burbach et al., 2009; Heinzerling et al., 2009). Skin-reactions can further be confirmed from blood analyses by quantifying species allergen antigens in the blood (Chabre et al., 2010). Controlled environment inhalation studies have also been conducted using isolated allergens or species pollen extracts to assess the allergenic response from individual species (Ørby et al., 2019, 2021). The benefit of this approach is the more realistic setting that can be extrapolated to real-life scenarios. The results from the above-mentioned test does not only infer species allergenicity but can also be further developed in an immunotherapy framework for species immunization (Jutel et al., 2005). Immunotherapy can provide some or total immunity for a limited time by injecting the sufferer with a standardized blend of allergens for a certain number of times until temporary immunity is achieved (Andersson and Lidholm, 2003). An alternative to injection is sublingual allergen immunotherapy (SLIT) (Demoly et al., 2015). There is some evidence to suggest that immunotherapy provides active long-term protection (Calderón et al., 2012; Durham et al., 1999). Standardized blends usually contain extracts from *Phleum pratense* (Kleine-Tebbe et al., 2006; Pilette et al., 2007) but has in recent years also contained extracts from *Lolium perenne* (Mösges et al., 2018; Sharif et al., 2019). Studies have shown that *Phleum pratense* allergen are sufficient in providing immunity to other temperate grasses due to extensive cross-reactivity with other species allergens, this will allow for monovalent immunotherapy (Aleksic et al., 2014; Hejl et al., 2009). Immunotherapy to subtropical grass allergens might require standardized blends from other subtropical grasses, although cross-over immunity has been found between temperate and subtropical grasses (Gangl et al., 2013; Nony et al., 2015). While these techniques are effective, they are not as common as utilizing antihistamines (Howarth and Holgate, 1984) or other Over The Counter (OTC) medication (Holgate and Polosa, 2008) for grass pollen symptoms during the pollen season (Cebrino et al., 2017). For pollen forecasters, medical professionals and researchers alike the easiest way to caution the sufferer of the upcoming (Kurganskiy et al., 2021) or current grass pollen season is to conduct standard pollen monitoring and to report the result to the public.

4. Aerobiology

4.1. Pollen monitoring

Grass pollen as a genus is monitored together with other aeroallergens using traditional and standardized techniques in national monitoring networks (D'Amato and Spieksma, 1992; Galán et al., 2014; Milic et al., 2020; Oteros et al., 2013). The primary role of the network is to monitor the aeroallergens in sufficient spatial resolution to allow for accurate pollen forecasts on a regional level based on the landscape heterogeneity on a national level (Suanno et al., 2021a). The secondary role is to provide warnings of coming seasons, based on pollen calendars from previous data, the current meteorological prognosis and phenological progression of the vegetation (Adams-Groom et al., 2020; Lo et al., 2019; Ríos et al., 2016). While the grass pollen season in a region tends to remain connected to the progression of the vegetation (bar long-distance transport (Estrella et al., 2006)) and thus generally stable over time, the seasons vary considerably between regions, countries and continents due to climatological and biogeographical factors (Emberlin et al., 2000; Galán et al., 1995; Valencia-Barrera et al., 2001; Waudby et al., 2022). In general, the grass pollen season is intimately linked with the growth season, as optimal temperature and precipitation brings on favourable germination, growth and flowering conditions (Davies et al., 2022; Gross et al., 2019; Minero et al., 1998; Recio et al., 2010; Schramm et al., 2021). Higher latitudes and altitudes tend to have a shorter growth season, and thus generally a shorter pollen season and lower pollen concentrations (Beggs et al., 2015; Smith et al., 2009). This is only true to some extent, as longer growth periods do not necessarily mean longer pollen seasons or higher pollen concentrations, as other more localized geographical factors will determine the abundance of grass pollen (Oteros et al., 2019). However, latitude is directly connected with the start of the season, as the growth season tends to start earlier at lower latitudes (Emberlin et al., 2000; Zhang et al., 2015).

Remote sensing technology (e.g., satellite imagery) is an effective tool for tracking the growth season in grassland systems (Ali et al., 2016; Vrieling et al., 2018), as it can be used as a proxy for the progression of grass pollen seasons (Khwarahm et al., 2017). Remote sensed vegetation indices (e.g., NDVI and EVI) have been used to quantify the phenological development of the vegetation and then link this with the grass pollen season (Devadas et al., 2018; Rojo et al., 2022; Skjøth et al., 2013). There has also been recent development in the use of high-resolution phenological

cameras (PhenoCams) and the green chromatic coordinate (GCC) index to monitor grass vegetation in connection with flowering and pollen variations (Liu, 2021; Watson, 2017). These approaches make remote sensing technology a cost-effective tool to monitor long-term change in growth seasons and land-use (Aasen et al., 2020; Horion et al., 2019).

Long-term research has shown that there can be considerable variation to the local pollen season, including onset of season, Seasonal Pollen Integral (SPIn) and season duration, which vary between years due to variations in local weather conditions but also climate change affecting the growth of the flora (Adams-Groom et al., 2022; Ariano et al., 2010; Bruffaerts et al., 2018; de Weger et al., 2021; Fitter and Fitter, 2002; Frenguelli, 2002; Gehrig and Clot, 2021; Ghitarrini et al., 2017b; Glick et al., 2021; Hoebeke et al., 2018; Jochner-Oette et al., 2019; Karatzas et al., 2019; Lind et al., 2016; Medek et al., 2016; Ruiz-Valenzuela and Aguilera, 2018; van Vliet et al., 2002; Ziska et al., 2019). While the investigation and subsequent understanding of the grass pollen seasons are well-developed for much of Western Europe, Northern America and parts of Asia due to extensive pollen monitoring networks (Buters et al., 2018), a lot of information is missing in the global perspective. This has made it difficult to connect and build understanding of the ecological processes involving meteorology, biodiversity and biogeography on a global scale and how these factors link with atmospheric grass pollen levels. Furthermore, grass pollen studies might not be high priority in some regions due to poor grass performance from unsuitable climate, poor habitats, short growth seasons or low allergenicity grasses (García-Mozo, 2017; Popescu, 2014; Singh and Mathur, 2012). Although the connection between biodiversity and pollen concentrations remains largely unexplored, as more diverse species communities have not been linked to increased pollen levels, arguments have been made that increased species richness can prolong the pollen season due to the sequential flowering of species (León-Ruiz et al., 2011; Medek et al., 2016).

The lack of studies on the global scale is partly due to the intensity and time-consuming aspect of manual pollen sampling. Recent advancements in bioimaging, laser optics, fluorescent spectrometry and machine learning has contributed to a new generation of real-time automatic pollen samplers (Buters et al., 2022; Markey et al., 2022; Maya-Manzano et al., 2023; Mills et al., 2023; Pöhlker et al., 2013; Swanson et al., 2022; Tummon et al., 2021). These approaches are likely to revolutionize the pollen monitoring field due to the drastic minimization of manual labour and man-hours required for daily monitoring. Examples of leading samplers include the Rapid-E from Plair (Switzerland) (Šauliene et al., 2019), BAA500 from Hund Wetzlar (Germany) (Plaza et al., 2022), KH-3000 from Yamatronics (Japan) (Miki et al., 2017), Polleno from Swisens (Switzerland) (Sauvageat et al., 2020) and WIBS from Droplet (USA) (O'Connor et al., 2014a). Some evidence exists that it is possible to distinguish grass pollen species with fluorescent spectrometry (O'Connor et al., 2014b; Pöhlker et al., 2013), but this has yet to be implemented successfully in large-scale monitoring programs. Although these automatic samplers combine various techniques to automatically classify and quantify various pollen with high accuracy, including grass pollen (Schaefer et al., 2021), they are currently unable to identify grass pollen to species level (mostly) due to the lack of distinct species pollen morphology.

4.2. Pollen morphology

Pollen monitoring networks utilize light microscopy and palynological methods to identify pollen taxa from aerial samples. Most taxa can only be identified to family or genus levels or even 'type' (e.g., as in the case with Cupressaceae/*Taxus* type). For example, due to overlapping size distributions and general lack of distinct morphological traits on a genus level (Jaeger, 2008; Morgado et al., 2015), only the grass family are usually counted. Although there might be small identifiable differences (Perveen, 2006), such as in the case of *Secale cereale* (rye) that is routinely recorded at some pollen monitoring stations (Kasprzyk, 2006; Kasprzyk et al., 2001).

Size differences can be used to separate regular sized natural grasses and larger sized pollen from cultivated grasses (e.g., cereals (Joly et al., 2007; Köhler and Lange, 1979)) and bamboos (Salgado-Labouriau and Rinaldi, 1990). Some size differences have also been identified between C3- and C4-grasses, making it possible to separate them morphologically to some extent (Jan et al., 2015). For most other grasses their size distribution exists on a spectrum (~15–40 μm), with on average smaller and larger pollen identified at a species level (Radaeski et al., 2016; Ullah et al., 2021; Yasniuk et al., 2020), but no precise way of separating them from the overall distribution. For example, the pollen from the subtropical grasses *Cynodon dactylon* range from 24 to 32 μm with an average of 28 μm, *Eragrostis bahiensis* 22–33 μm, average of 29 μm and *Paspalum notatum* 32–39 μm, average of 34 μm (Radaeski et al., 2016).

The size of a pollen grain is inherently linked with its density and weight and thereby its gravitational settling velocity and potential for atmospheric transport (Borrell, 2012; Durham, 1943; Lin et al., 1994). Smaller pollen could be transported further but might also contain less overall weight of potential allergens due to their size, making them theoretically less allergenic but more wide reaching. However, this has not been tested and the practical implications of this remains under-studied. In theory, by knowing the statistical properties of multiple species size distributions, it should be possible to assign species likelihoods from a mixed aerial sample (Takahashi et al., 1995), although such a method would only be at best an educated statistical guess. Even pertaining to a random sample containing an unlikely low number of species would be uncertain (Fig. 3). Another more reliable method of establishing species contribution in a probabilistic framework is by quantifying pollen production.

4.3. Pollen production

Grasses employ wind and atmospheric air currents to disperse their pollen (anemophily) and achieve successful reproduction (Cresswell et al., 2010; Timerman and Barrett, 2021). Anemophily is primarily a numbers game, due to the inherently random nature of moving pollen from anthers to pistils of the same species using the air as a vector (Friedman and Barrett, 2009; Friedman and Harder, 2004). The evolutionary consequence of this is higher pollen production in order to increase the reproductive success rate, with widely varying total pollen not only per species but also within species per anther (Aboulaich et al., 2009; Ali et al., 2022; Severova et al., 2022; Subba Reddi and Reddi, 1986). The practical implication of this, all else being equal, is pollen from species with high pollen production being statistically more likely of being encountered in the atmosphere.

Pollen production is usually treated loosely as a function of the number of pollen per anther, the number of flowers per inflorescence and the number of inflorescences per plant (Prieto-Baena et al., 2003). Furthermore, pollen production via flower production is mediated through environmental suitability, resource accumulation and plant abundance (Jung et al., 2021). Therefore, on an area basis, abundant species with low environmental requirements and high capacity to accumulate resources should far outperform more specialised species and dominate the atmospheric biodiversity abundance. This is inherently linked with the other allergenic qualities mentioned above as e.g., one of the higher pollen producing genera, *Sorghum* (Prieto-Baena et al., 2003), has been shown to have highly allergenic pollen (Bokka et al., 2019; Sridhara et al., 2002, 1995). However, higher pollen production does not necessarily mean higher allergenicity, as another high pollen producing genus, *Trisetaria* (Prieto-Baena et al., 2003), is generally not considered allergenic. Although, as mentioned previously, this could be biased due to under-investigation. The link between high pollen production mediated via exposure likelihood and allergy remains largely under-studied, though exposure likelihood has previously been suggested to be a contributing factor to allergenic sensitivity (Barber et al., 2008; Behrendt and Becker, 2001; McKenna et al., 2016). Grass abundance and management are here relevant considerations, as widely cultivated uncut forage grasses would produce magnitudes more pollen than natural grasses, although forage grasses are usually cut before flowering for increased palatability and nutrient profiles (Fuglie et al., 2021; Lindström et al., 2014). Allergy via pollen production is neither genus-exclusive, as the annual *Poa annua* has lower pollen

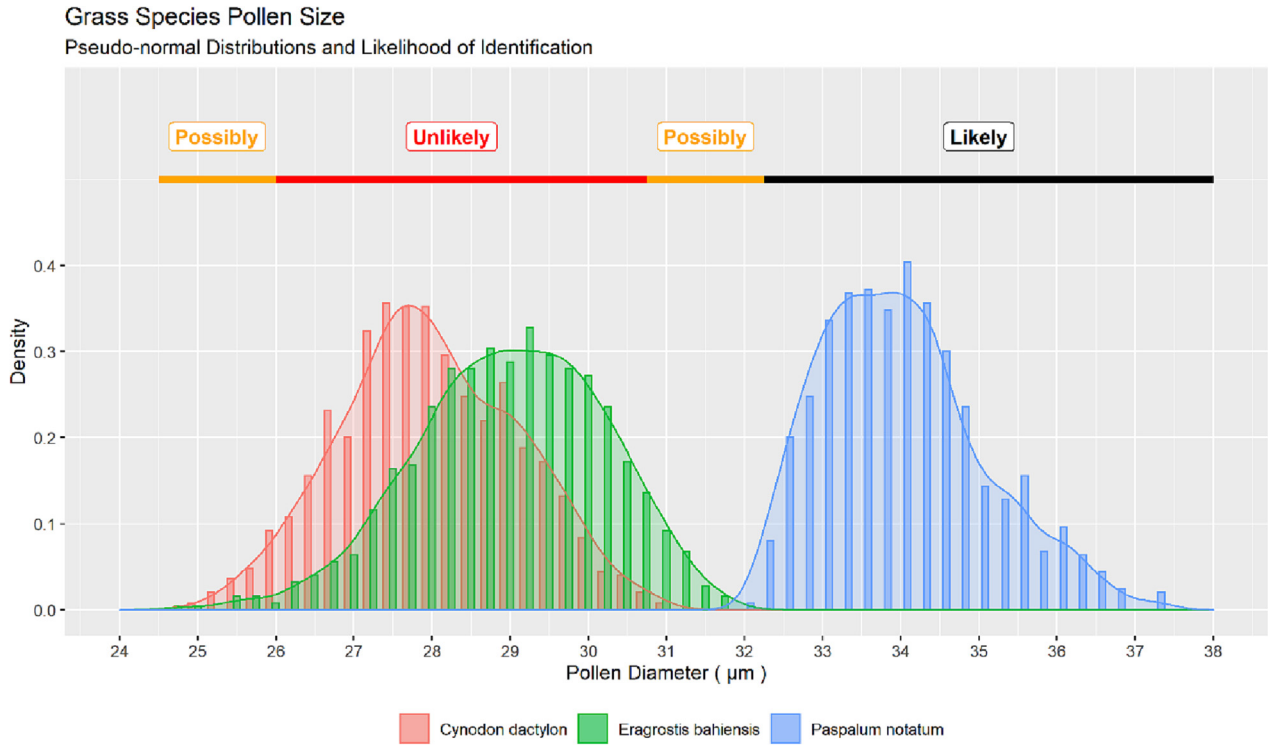

Fig. 3. Pseudo-normal distribution of pollen diameter of three common allergenic subtropical grasses (*Cynodon dactylon*, *Eragrostis bahiensis* and *Paspalum notatum*) and the size distribution overlap in terms of likely species classification from a random atmospheric sample.

production than the perennials *Poa pratensis* and *Poa trivialis* (Severova et al., 2022). Although the allergens in *Poa pratensis* have been examined to some extent in the past (Chakrabarty et al., 1981; Ekramoddoullah et al., 1980), the general allergenicity has not been determined, with one recent study suggesting that the species is not allergenically harmful (Rowney et al., 2021). Even though pollen monitoring, morphology and production cannot identify the individual species contribution to the atmosphere, combined they provide a reasonable indication of when and what pollen should be there (e.g. Ghitarrini et al., 2017a; León-Ruiz et al., 2011; Prieto-Baena et al., 2003). Combining these methods with flowering phenology on a species-level has previously been the main way to investigate where the pollen originated.

5. Flowering phenology

5.1. Phenological classification

Multiple methods of phenological classification have been applied to flowering grasses. Flowering in the context of pollen release is distinct from heading, the creation and presence of flowering heads, and is instead normally acknowledged by the initial extrusion of male anthers, the pollen-containing reproductive organs. This is generally referred to as first flowering, the start of the flowering season, and is classified binomially as yes or no and can vary considerably between regions (Bartošová et al., 2015; Estrella et al., 2006; Kožnarová et al., 2011). Alternatives to anther extrusion is the observation of pollen release (Tormo et al., 2011) or open flowers (León-Ruiz et al., 2011). Flowering in grasses has been shown to be useful in quantifying effects from climate change (Dunnell and Travers, 2011; Munson and Long, 2017; Richardson et al., 2013; Sherry et al., 2007) partly due to observational simplicity and long-term record (Tooke and Battey, 2010). For the potential of pollen release, flowering is normally categorized as a spectrum ranging from heading (pre-flowering) to senescence (flowering head desiccation).

The most used observational approach in categorizing the phenological spectrum of grasses is the Biologische Bundesanstalt, Bundessortenamt und Chemische Industie (BBCH) system (Meier, 2018). The system was originally developed by and for agricultural practitioners to discern and record phenological development in a wide range of crops and consists of multi-stage development expressed as a two-digit code. The code corresponds to a primary growth stage and a secondary growth stage within the primary one (Hess et al., 1997; Hong et al., 2011; Meier et al., 2009). For flowering grasses, the crop type 'cereal' and the primary growth stage 'flowering' have been utilized (Cornelius et al., 2014, 2011). The original secondary growth stages in the classification were the beginning of flowering, full flowering and senescence, but the method has been readily refined and extended to focus on the fractional and incremental extrusion of anthers (Fig. 4). This has allowed for a more detailed and specific progression of the numbers of anthers being capable of releasing pollen (Ghitarrini et al., 2017a). Other similar methods have been developed and explored as well, e.g., Giardini Fenologici Italiani (GFI) (Malossini, 1993), with the methods having been shown to overlap in stage correspondence and therefore observational accuracy (Puppi and Zanotti, 2011). For this type of phenological spectrum observation to be representative at one location a large number of individuals should be classified simultaneously.

5.2. Population dynamics

Flowering, as with many other biological traits, is determined and influenced by genetic and environmental variation on an individual plant level (Visser et al., 2010). The practical implication of this is slight variation in the expression and timing of the process, generally giving rise to normally distributed responses on a population level (Kendall and Fox, 2002). Population in this context is a cohesive unit in time and space rather than a genetically distinct one. One of the consequences of the normally distributed response is that most individuals are expected to act similarly due to a certain set of circumstances, while some individuals may behave differently (Miller-Rushing et al., 2008), e.g., start flowering a day earlier or later than the average of the population. While a normalized response can be accounted for to some extent by modelling influential factors, for example temperature and precipitation for flowering, the potential for random and

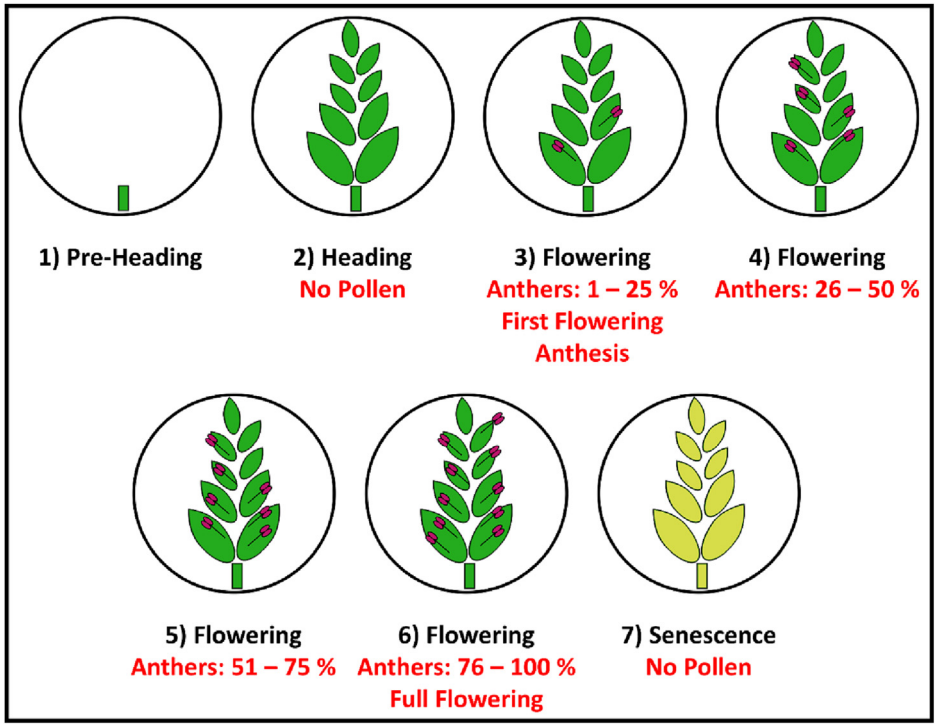

Fig. 4. Spectrum of phenological development according to the BBCH system and the generalized crop 'Cereal' applicable to flowering grasses categorized from pre-heading to senescence. BBCH codes of stages exemplified: 1) BBCH <60, 2) BBCH 60, 3) BBCH 61, 4) BBCH 63, 5) BBCH 65, 6), BBCH 68 and 7) BBCH 69.

unquantified variation at an individual level will always remain (Forrest and Miller-Rushing, 2010), e.g., due to micro-meteorology or resource accumulation via soil heterogeneity. Therefore, observing a larger fraction of a population will increase the likelihood of quantifying the overall response and distribution of their population dynamics, which will allow for higher accuracy in predicting the population behaviour (Fox and Kendall, 2002). This is especially relevant for grasses, as their flowering progression and pollen release potential can vary widely between individuals and change rapidly from one day to the next, as previously observed in *Dactylis glomerata* (Frisk et al., 2021; Tormo-Molina et al., 2015). However, to what extent populations, species and genera diverge in their within-population responses has not been fully explored, neither have the relevant factors that impact upon them. While the within-population variation remains uncertain, progress has been made to characterize species variation in the general flowering season, and in what order species are likely to flower.

5.3. Seasonal sequential flowering

The optimal flowering time of grass species is determined by their ancestral evolutionary environment and modulated by optimal meteorology through the life cycle. Their evolutionary past through niche partitioning and resource optimization shaped grass clades (BOP and PACMAD) to flower based on the requirements of their adapted environment, primarily via photoperiodism and precipitation availability (Preston and Fjellheim, 2020). Temperate grasses (mainly BOP-clade) normally have long-day induction and flower when temperatures and light conditions are optimal for growth in temperate regions during late-spring to mid-summer (Fjellheim et al., 2014). This contrasts with subtropical grasses (mainly PACMAD-clade) that normally have short-day induction and flower during the end of the summer, primarily to optimize water availability during the start of the rainy season in otherwise warm and dry conditions (Doust et al., 2017; Edwards and Smith, 2010; Tainton, 1969). Although the grass flora in some areas consists of a mix of both clades, most grass communities are dominated by one or the other (Medek et al., 2016; Preston and Fjellheim, 2020). The timing of the growth and reproduction cycles of the vegetation within each period is further dependent on precipitation, temperature and solar radiation variability (Romero-Morte et al., 2020), as many grasses require a species-specific number of growing degree days (GDD) over a specific temperature threshold to reach the reproductive stages of their development (Abel et al., 2018; Buxton and Marten, 1989; Frank and Bauer, 1995; Moore and Moser, 1995). The GDD and induction timing are connected physiologically and varies between species, with some responding stronger to light, contributing to more consistent flowering time (Colasanti and Coneva, 2009; Cooper and Calder, 1964; Heide, 1994).

In Europe, where species belonging to the temperate BOP-clade are the most common, multiple studies have been conducted to identify how spatiotemporal flowering on a species and community level corresponds to the fluctuations of the grass pollen season. The studies have primarily been conducted in Spain (Cebrino et al., 2018, 2016; León-Ruiz et al., 2011; Rojo et al., 2017; Romero-Morte et al., 2020, 2018; Tormo et al., 2011), with additional studies in countries such as Italy (Frenguelli et al., 2010; Ghitarrini et al., 2017a), France (Grégori et al., 2019), Germany (Estrella et al., 2006; Jochner et al., 2012) and Austria (Kmenta et al., 2017, 2016). However, the earliest study connecting community grass flowering, pollen abundance and symptom data was conducted in Paris in 1987 (Ickovic et al., 1989).

In general, some patterns in the sequential flowering have been observed: *Bromus*, *Hordeum* and *Alopecurus* species tend to flower in the early part of the season, followed by *Lolium*, *Dactylis*, *Festuca* and *Poa* species in the late-early to middle of the season and *Phleum* and other PACMAD species, such as *Cynodon*, flowering towards the latter half of the season. *Lolium* species tend to have longer active flowering times, likely being able to release pollen during extended periods of time. Furthermore, within-genus variation in flowering time seems to be low, as multiple species in the genera *Bromus* and *Hordeum* have been observed to flower simultaneously (León-Ruiz et al., 2011; Romero-Morte et al., 2018), although more research is needed to confirm this pattern with larger species pools and additional genera. The peak of the grass pollen season tends to coincide with the full flowering (theoretically maximum pollen release potential) of *Lolium*, *Dactylis*, *Festuca* and *Poa* species, suggesting that these

genera on average contribute more pollen than other species (Ghitarrini et al., 2017a; Kmenta et al., 2017; Tormo et al., 2011). However, many other species tend to also flower at the same time, making the species distinction difficult due to the overlap (Cebrino et al., 2016; Minero et al., 1998). There is also considerable variation in phenological progression between years and habitats depending on which species are present, meteorological conditions and climate change (Cebrino et al., 2018), although this has primarily been observed in agricultural species and cultivars, e.g., *Hordeum vulgare* (barley) and *Triticum aestivum* (wheat) (García-Mozo et al., 2010b; Oteros et al., 2015).

While observations of grass flowering on a community level are sparse for the rest of the world, as grass species are normally treated generically in analyses, some studies are available from the United States (Craine et al., 2012), India (Munshi, 2000; Parihar and Pathak, 2006) and Australia (Tng et al., 2010; Tothill, 1977). In these regions the same pattern of early temperate grass flowering and late subtropical grass flowering can be observed. For example, temperate *Bromus*, *Hordeum* and *Poa* are observed flowering early in the season while subtropical *Bothriochloa*, *Brachiaria*, *Pannisetum* and *Paspalum* flowering later. Within-genus flowering time variation is also observed to be low in multiple genera, e.g., *Agrostis*, *Bromus*, *Bothriochloa* and *Digitaria.* However, it varied considerably in the temperate *Poa* (Munshi, 2000) and subtropical *Brachiaria* (Parihar and Pathak, 2006), although this could be due to environmental variation, as the *Poa* species observed were spread altitudinally and the *Brachiaria* species experienced monsoonal conditions (Gadgil, 2003) which likely affected their respective growth conditions.

The sequence of flowering is not only relevant to investigate species contribution to the atmosphere, but also in determining the likely order of exposure. To what extent grasses that flower the earliest in the season, e.g., *Anthoxanthum*, *Alopecurus* or *Bromus* have a seasonal priming effect on the immune system of the sufferer remains unclear, or if other related particles could be relevant in this process (Beggs, 1998; Gilles et al., 2012). While grass flowers are the source of the pollen, investigating how the pollen travels from the flower to the atmosphere and where it ultimately ends up is essential in determining the absolute reach of each species.

5.4. Release and dispersion processes

In general, pollen release occurs when the mature anther reaches a sufficiently desiccated state (Huang et al., 2004; Keijzer et al., 1996; Matsui, 2000), balanced by the drying properties of air temperature, solar radiation and low relative humidity and encouraged by wind speed. Vapour-pressure deficit (VPD) has previously been used to describe the water balance determining pollen release in grasses (Viner et al., 2010). The reduced water status causes anther dehiscence, the anther splits and the pollen is dispersed (Wilson et al., 2011) and modulated by wind speed. In theory, the process should occur in most species during mid-morning due to increased temperatures, increased solar radiation and reduced relative humidity caused by the rising sun. However, earlier studies have observed that pollen release varies widely between species, although most species were observed to have a preferred time, even if that time differed (Bhattacharya and Datta, 1992; Hyde and Williams, 1945; Liem and Groot, 1973; Subba Reddi et al., 1988). Extruded anthers might not be capable of releasing pollen instantly after being extruded, creating a potential delay between anthesis and pollen release. This could contribute to the species differences, but the practical importance of this delay and to what extent genetic and taxonomical differences are underpinning it remains largely unexplored.

Information on species-specific grass pollen dispersal is limited, with some studies having investigated *Lolium perenne* (Giddings, 2000; Giddings et al., 1997a, 1997b) and *Festuca pratensis* (Nurminiemi et al., 1998; Rognli et al., 2000) in relation to geneflow of genetically modified grasses and potential factors influencing the transportation distance. The studies found that <10 % of grass pollen are dispersed further than 100 m from the source area and <5 % further than 200 m. Furthermore, one recent study found that only small proportions of *Festuca rubra* pollen are dispersed further than 300 m from an isolated source population (Frisk et al., 2023). This corresponds with older research conducted on prairie grasses such as *Agropyron cristatum*, *Bromus inermis* and *Thinopyrum intermedium* (Jones and Newell, 1946) and the subtropical *Paspalum notatum* (Hodgson, 1949). However, later studies have also shown that grass pollen can be dispersed much further, up to 30 km, depending on the atmospheric conditions (Frisk et al., 2022; Viner et al., 2017; Viner and Arritt, 2012; Watrud et al., 2004). This has contributed to the general understanding that pollen samplers can adequately capture the grass pollen season within the regional 30 km area (Katelaris et al., 2004; Pashley et al., 2009). This apparent inequality has been reconciled by acknowledging the importance of pollen dispersal from the local flora to the local landscape, but that smaller fractions can escape to the regional landscape (Hjort et al., 2016; Skjøth et al., 2013; Werchan et al., 2017). To what extent differences in pollen diameter and density as seen between species will influence the dispersal distance has not yet been fully explored. Likely the main reason for this knowledge gap is the difficulty in conducting isolated species experiments in a natural environment, but new advancements in eDNA and molecular genetics have provided methods to isolate individual species in atmospheric community samples.

6. Molecular identification

Environmental DNA (eDNA) constitutes any unspecific genetic sample collected from the environment using either active or passive sampling methods (Creer et al., 2016). After the samples have been collected and processed they can be used to test a variety of hypotheses, primarily related to presence, abundance and biodiversity of various organisms. In the context of grass pollen three main analytical methods have been utilized: DNA metabarcoding, quantitative real-time polymerase chain reaction (qPCR) and enzyme-linked immunosorbent assay (ELISA). DNA metabarcoding is a semi-quantitative method used to estimate relative abundance of specific community taxa based on specific genomic regions and processed through bioinformatics (Kraaijeveld et al., 2015). While the method can provide relative abundance in community samples with good accuracy, the understanding of the connection with biomass and absolute abundance is still limited (Creer et al., 2010; Lamb et al., 2019). The genomic regions most used for this purpose are ITS, *rbc*L, *trn*L and *mat*K (Baksay et al., 2020; Hawkins et al., 2015). qPCR is a quantitative method used to isolate species-specific presence and abundance (Bustin et al., 2005). ELISA is a quantitative immunological method that can detect presence and abundance of species-specific allergens (Crowther, 2000; Duffort et al., 2004). Each method has unique advantages and disadvantages and specific processing protocols that have been reviewed elsewhere (Núñez et al., 2016).

DNA metabarcoding has been used to investigate the spatiotemporal composition of the grass pollen season due to the ability to distinguish individual taxa in community samples. This has primarily been conducted on a genus level rather than a species one due to lack of discrimination and incomplete genomic taxonomical reference databases (de Vere et al., 2012; Somervuo et al., 2017). There is also a cost pressure attached to the metabarcoding of plants, as it is strongly recommended to use two DNA regions for the barcoding process due to low variability, essentially doubling the costs compared to animal barcodes (Chase et al., 2005; Kress et al., 2005; Rubinoff et al., 2006). One recent study has used metabarcoding to reveal the atmospheric dominance of *Alopecurus*, *Festuca*, *Holcus*, *Lolium* and *Poa* on a national level in the United Kingdom (Brennan et al., 2019). Furthermore, *Chloris*, *Cynodon*, *Megathyrsus*, *Paspalum* and *Triticum* have been found to be major components of the Australian atmospheric diversity (Campbell et al., 2020). On a more localized scale, Frisk et al. (2023) found that the grass pollen season in the United Kingdom was dominated by six genera: *Agrostis*, *Alopecurus*, *Arrhenatherum*, *Holcus*, *Lolium* and *Poa*, while simultaneously identifying that the grass pollen biodiversity varied widely at the micro-scale (<300 m) environment. Multiple studies have found the method to be representative when comparing it to known species compositions, although differences have been observed depending on the genomic region analysed (Omelchenko et al., 2022). Optimization will be key in improving the overall accuracy of the species identification, as methods are

still being refined (Bell et al., 2019; Leontidou et al., 2018) and reference databases extended to include more species sequences (Banchi et al., 2020a; Dormontt et al., 2018). Currently, one key drawback is the temporal resolution, since multiple days of atmospheric samples are needed to be pooled to accumulate sufficient DNA for analysis. This issue however is likely to improve with time as newer techniques, e.g., MinION sequencing, allow for smaller quantities of DNA (Peel et al., 2019). Overall, the method is seen as a viable complementary tool to pollen monitoring since it can increase the taxonomical resolution and accuracy of atmospheric samples (Banchi et al., 2020b; Bell et al., 2016; Hanson et al., 2022; Johnson et al., 2021).

qPCR, although not as utilized as metabarcoding in terms of atmospheric grass pollen flora, has shown to be a useful tool in exploring the difference in spatiotemporal abundance between taxa (Ghitarrini et al., 2018; Rittenour et al., 2012; Teng et al., 2016). The under-utilization likely stems partly from the lack of specificity in species primers, causing an overestimation of true species abundance and therefore a drop in overall accuracy (Bustin and Huggett, 2017). However, one study connected the abundance of species-specific grass pollen on a national level in the United Kingdom to hospital emissions of asthma and prescription rates of respiratory drugs and found that increases in *Cynosurus cristatus* and *Phleum pratense* pollen were associated with a significant increase in negative respiratory conditions (Rowney et al., 2021).

In a similar context, ELISAs have been used to quantify free allergens in atmospheric samples and explored how the presence of allergens are connected to the general pollen season (Buters et al., 2015). Since allergens are likely to originate from one species or genus it can give a reasonable assumption of taxonomical association of the observed grass pollen. Most studies have investigated the abundance of Lol p1 (*Lolium*) (De Linares et al., 2010; Fernández-González et al., 2011) and Phl p5 (*Phleum*) (Alan et al., 2018; Bastl et al., 2016; Buters et al., 2015; Jochner et al., 2015; Maya-Manzano et al., 2022; Ščevková et al., 2020) but other allergens and species have been studied as well (e.g., *Trisetum paniceum* (Cabrera et al., 2002), *Cynodon dactylon* (de Souza et al., 2021) and Phl p1 (De Linares et al., 2014)). Although the observed allergens must by causation be associated with grass pollen many studies have found that species-specific free allergen concentrations vary independently of grass pollen concentrations. This suggests that either the individual species abundance of the associated allergen is not representative of the general grass pollen season, or that there exists divergent mechanisms that separate the grass pollen abundance to the allergen abundance (Beggs, 1998). This has cast doubt on the origin and airborne duration of free grass allergens, which could relate to the flowering of individual species. Observations of simultaneous multi-species allergens and species-specific grass pollen abundance via qPCR could shed further light on this divergence.

7. Conclusions and recommendations for future research

Throughout these sections we have provided open-ended questions and marked areas of uncertainty that require further exploration. Three main gaps in knowledge have been found to permeate the field which need to be addressed to elucidate the species contribution to grass pollen allergy:

Firstly, the association between allergen homology and how it is reflected in grass taxonomy must be identified. Currently, it is uncertain how representative each identified allergen is within different taxonomical units such as populations, species and genera. Further research is needed to understand if the allergen Phl p5 for example only occurs in the species *Phleum pratense*, to what extent it occurs in multiple species in the genus and if the allergen production varies between populations or biogeographical continents.

Secondly, understanding the importance of pollen morphology of different grass species in terms of dispersal capacity, primarily diameter and density, is essential in determining the representative spatial range of species. Access to this information will facilitate mechanistic connection between species source maps and atmospheric transportation models that is currently missing.

Lastly, further research is needed to identify how the flowering of different species is reflected in the atmospheric community composition on multiple spatial scales. Only by knowing the temporal component and any potential delays in pollen transportation from anther to atmosphere can we systematically connect the biosphere to the atmosphere.

In general, future studies should enhance holistic study design to promote synergy between the multiple distinct interdisciplinary fields of research, only then can the grass species element be fully understood (Davies et al., 2015), and allergy effectively mitigated especially in relation to projected increases in temperature and atmospheric concentrations of CO_2 due to anthropogenic climate change (IPCC, 2022).

CRediT authorship contribution statement

Carl A. Frisk: Conceptualization, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. **Beverley Adams-Groom:** Investigation, Writing – review & editing. **Matt Smith:** Investigation, Writing – review & editing.

Data availability

The authors do not have permission to share data.

Declaration of competing interest

The authors declare that they do not have any inappropriate financial or personal relationships that would bias or influence the research in this paper.

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