

CME review

Aeroallergen botany

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Learning Objectives:

At the conclusion of this activity, participants should be able to:

- Describe the development of plant pollination and its variants as well as the differences between wind-pollinated and insect-pollinated plants
- Discuss the impact of climate change on aeroallergenic plants

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Introduction

Vascular plants propagate through the extension of roots, shoots, and rhizomes and by seed or spore. Transport of pollen, the male gamete, to the ovary, the female gamete, results in sexual

reproduction. Pollen dispersal mechanisms may be with the wind (anemophily), water (hydrophily), or through a vector such as an insect (entomophily). Insect-pollinated plants are not commonly inducers of hay fever but can be. Some plants use the 2 mechanisms, being pollinated primarily by insects but producing sufficient pollen that it becomes airborne (amphiphily). This review addresses the evolution of pollination techniques, characteristics of anemophilous plants, North American floristic zones, respirable pollen particles, and the impact of meteorologic parameters and climate change on pollen dispersal.

Evolution of Pollination

With the evolution of seed plants, these new types of vegetation removed the need for water transport of gametes for reproduction. No longer was close proximity to open water necessary for propagation, allowing vast expansion over the prehistoric landmasses.¹ The earliest seed plants were gymnosperms, characterized by naked seeds. The investigation of the fossil record and examination of extant gymnosperms suggest that these plants have always relied on wind pollination for reproduction. This is in distinction to the later developing angiosperms, or flowering plants, which from the time of their origin were vector—primarily insect—pollinated. It is estimated that 10% to 16% of all extant angiosperms are wind pollinated: in contrast to gymnosperms, this represents a later evolutionary development.^{1,2} Charles Darwin studied floral biology for more than 40 years and in 3 texts made seminal observations on the impact of crosspollination (vs self-pollination) on plant fitness and propagation.³ He believed strongly that this crossfertilization was aided by insect pollination. In 1876, he stated: “As a large quantity of pollen is wasted by anemophilous plants, it is surprising that so many vigorous species of this kind abounding with individuals should still exist in any part of the world. ...It seems at first sight still more surprising fact that plants, after having been once rendered entomophilous, should ever again have become anemophilous.”⁴ This suggests that, despite appearing a very inefficient method, wind pollination must have advantages in certain scenarios, especially in regions where animal vectors may be less common.

Modes of pollination are listed in Table 1. Abiotic dispersal of pollen does not require involvement of an animate intermediary, relying instead on a physical factor, ie, wind or water, for transport. The latter is very rare: most aquatic flowering plants have inflorescences above water level and rely on wind or an animal vector.

Progymnosperms developed in the late Devonian period approximately 380 million years ago (mya), with true gymnosperms apparent in the mid-Carboniferous period 320 mya. These were wind pollinated, but pollen capture was aided by the secretion of a “pollination drop,” which could trap grains and provide an avenue of approach to the ovule. This pollination drop exists in numerous gymnosperms, but also in *Ginkgo biloba*, a tree believed to be evolutionarily basal to the conifers.⁵ However, there is evidence that members of 3 extinct families of scorpion flies fed on

gymnosperm pollination drops and aided with pollination in the middle Jurassic period 170 mya, at least 30 million years before the development of angiosperms.⁶

Pollination facilitated by an animal vector appears to have greatly expanded 140 mya in the early Cretaceous, the period after the Jurassic, concomitant with the explosive development of angiosperm plants.⁷ Even ancient relatives of extant wind-pollinated taxa such as *Platanus* (sycamore and plane tree) appear to have initially been insect pollinated.⁷ Basal eudicots were well established by 116 to 125 mya. The most likely early vectors were beetles, with bees not making an appearance until the late Cretaceous period, approximately 80 mya. Larger animal vectors, such as bats and birds, did not play a role until the following Tertiary era, approximately 30 mya.

Common Characteristics of Wind-Pollinated Plants

Although wind pollination appears to be a simpler process than vector-facilitated pollination, it is extravagant in requiring a large amount of pollen to be produced to ensure successful reproduction. In an extensive study of numerous trees and grasses, Erdtman⁸ showed that wind-pollinated plants produce extraordinary amounts of pollen. Birch and alder catkins may have more than 200 individual flowers. He reported that a single birch catkin produced approximately 6 million pollen grains and an alder catkin produced approximately 4.5 million. In turn, English oak catkin released up to 1.25 million grains. He calculated the number of catkins per tree and estimated the amount of pollen produced. A birch tree released more than 5.5 billion grains over a single year, an alder 7.2 billion, and an oak significantly less at a little over half a billion grains. Spruce, similar to birch, produced approximately 5.5 billion grains in a year. Cereal rye grass contained 4.25 million pollen grains per inflorescence.⁸

A perfect flower contains male and female reproductive structures. The male portion is the stamen, consisting of a stalk or filament, and the anther, or pollen sac containing the grains, or male gametes. Arising from the female ovary is another stalk, or style, which ends in a pollen-receiving surface, the stigma. Most perfect flowers have showy petals, sepals, and nectar-producing glands to act as attractants for vectors. Common characteristics of wind-pollinated plants are listed in Table 2. Such plants tend to have incomplete flowers, with male and female functions found on separate structures, although plants with perfect flowers also may be effectively wind pollinated. The pollen-producing flowers are exposed to the wind. On taller plants or trees, this is frequently on dangling catkins, as described by Erdtman.⁸ On herbaceous plants, the inflorescences are thrust up into the air on the higher portions of the plant. Female flowers may be lower, at the base of stems or at axils of leaves, or even found on separate plants (dioecy). Showy petals and sepals are insignificant or absent, and attractants such as color, fragrance, or nectar are absent. The pollen grains tend to be small and dry, with a less adhesive coating such as pollenkitt, and with decreased ornamentation to minimize turbulence in the air.⁹

Pollen clumping, in which large numbers of pollen grains are released en masse and stick together, has long been assumed to be characteristic of entomophilous plants. Simultaneous transfer of a large number of grains by an insect presumably would facilitate crosspollination. However, it was believed to be detrimental in

Table 1
Modes of pollination

1	Abiotic pollination
a	Wind (anemophily)
b	Water (hydrophily)
2	Biotic pollination
a	Beetle (cantharophily)
b	Butterfly (psychophily)
c	Moth (phalaenophily)
d	Bee (melittophily)
e	Fly (myophily/sapromyophily)
f	Bird (ornithophily)
g	Bat (chiropterophily)

Table 2
Characteristics of wind-pollinated (anemophilous) plants

Incomplete flowers—spatially separate male (staminate) and female (pistillate)
Male flowers (stamens) exposed to wind
Petals and sepals inconspicuous or absent
Absent vector attractants, eg, color, aroma, or nectar
Pollen grains small, dry, with decreased surface ornamentation

wind-pollinated plants because the clumps, being heavier, would disperse shorter distances than single airborne grains. However, such clumps have been observed in dispersion studies of some widely distributed anemophilous plants. A study of short ragweed (*Ambrosia artemisiifolia*) showed clumps could be advantageous, with initial clumps pollinating the parent plant population, whereas smaller airborne clumps resulting from the breakup of larger clumps would remain afloat and crosspollinate distant populations.²

In 1931, Thommen¹⁰ set out 5 necessary principles for a plant to be an important inducer of pollinosis (Table 3). Referred to as Thommen's Postulates, they continue to be generally correct, although with some modifications. The "excitant of hay fever" is most likely a rapidly elutable protein or glycoprotein, which also can be coated on respirable cytoplasmic particles. Buoyancy is affected by size, with most anemophilous pollens being 20 to 40 μm . In the proper setting, entomophilous plants can release sufficient airborne pollen to cause sensitization. A single point source, such as outside a bedroom window, could lead to individual sensitization. Although most pollen grains settle within meters of the source, pollens can be transported for hundreds or, occasionally, thousands of miles.^{8,11}

Floristic Zones

The distribution of individual plant species depends on many factors, such as average temperature ranges, prevalent humidity, and average rainfall. Soil conditions, such as density, mineral content, and pH, may provide selective advantages to different plants.¹² Certain widely distributed plants have adapted to diverse circumstances, whereas others are niche specific, adapting to extremes of temperature or water availability. The range of native indigenous species may be determined by niche selectivity. The extent to which an invasive plant can spread will be determined by its adaptability, aggressiveness, and length of time from introduction. Burning bush or summer cypress (*Kochia scoparia*) was introduced as an ornamental, quickly escaped cultivation, and is now found throughout North America.¹³ The other major tumbleweed of the Great Plains, Russian thistle (*Salsola kali*), was introduced as a contaminant of flaxseed in Bon Homme County, South Dakota in 1886; it quickly spread over the entire Great Plains, western states, and Canada.¹⁴ In similar fashion, short, giant, and western ragweed (*Ambrosia artemisiifolia*, *Ambrosia trifida*, and *Ambrosia psilostachya*, respectively) have been introduced into Europe and are now found throughout southern and central Europe.¹⁵ Sensitization to ragweed has greatly increased in Europeans.¹⁶

Floristic zones or regions were originally defined by their endemic flora.¹⁷ However, these plant niches are molded by physical factors, the most important of which is the annual mean minimum temperature. Based on the average annual minimum temperature, the US Department of Agriculture has defined 12 North American "hardiness zones," beginning with zone 0 at lower than -60°F and progressing by 10° increments to zone 11 at higher than 40°F .¹⁸ There are 6 additional factors affecting local climate: latitude, elevation, oceanic influence, continental air mass influence, mountains or hills, and local terrain features.¹² Increasing latitude results in longer and colder winters. For each rise of 1,000

feet in elevation, there is a 3°F decrease in temperature, which in North America equates to a northward shift of 600 miles. The ocean effect produces cooler summers and milder winters; large bodies of water such as the Great Lakes will have a similar effect. Owing to western prevailing winds in North America, the Pacific Ocean effect reaches farther inland than the Atlantic Ocean effect. In the central region, the continental air mass influence provides hotter summers and colder winters with more evenly spaced rainfall. Mountains and hills are barriers for precipitation, and the windward side will be wetter. Like water, cold air flows downhill, collecting in low points, such as creek beds, gullies, and ravines.

Takhtajan divided North America into 5 regions containing 13 provinces or zones and then divided several of these provinces into subprovinces or sectors, resulting in 20 zones.¹⁷ Figure 1 represents a modification of his system. The Arctic tundra is treeless, and vegetation is limited to grass and short shrubby growth. The Scandinavian and vast Canadian boreal forests have fewer weed and grass aeroallergens and a preponderance of conifers and northern deciduous trees, such as alder, aspen, and birch. The Appalachian eastern agricultural zone is characterized by marked diversity in trees and weeds and numerous "northern pasture grasses" of the subfamily Pooideae. The deciduous forests have been replaced in large degree by urbanization and farming activity. Certain native trees, such as elm and chestnut, have been decimated in their original ranges by different fungal blights. The Atlantic/Gulf coastal plain also shows great diversity among trees with the addition of southern trees, such as live oak and pine, and a preponderance of southern grasses, such as Bermuda, and *Panicum* grasses, such as Johnson grass. The Great Plains prairie is comprised of a great wedge beginning in Texas and extending northward across the middle of the continent through Manitoba to Alberta. Eastern reaches originally were tall-grass prairie, and reaches on the western higher elevation abutting on the Rocky Mountains were short-grass prairie. The Rocky Mountain Cordillera shows marked floral diversity owing to extreme changes in elevation and local terrain. The Sierra Madre is the Mexican equivalent to the Rocky Mountains. The Tamaulipas soil is rich in gypsum and shows flora adapted to these mineral conditions. The Vancouver Pacific maritime zone, although spanning marked changes in latitude, demonstrates the moderating effect of the Pacific current. The Sonoran Desert is lower in altitude than the Great Basin to the north and the Chihuahua Desert to the east. The latter 2 are colder, whereas the former desert is hotter. The Mojave Desert transitions between the Sonoran Desert and Great Basin and is divided between these 2 floristic zones. The southern region zones also transition from high desert to tropical lowlands. Although aeroallergenic plants are found in the tropical zones, pollens are weaker inducers of symptoms compared with mold spores and perennial allergens, such as dust mites, owing to the impact of increased humidity lowering airborne pollen concentrations and the presence of numerous animal vectors facilitating entomophily.^{19,20}

The "urban forest" may defy limitations of the floristic zones in which those cities are found. Urban planning of city parks and selection of street trees frequently incorporates nonendemic species. Survival of more southerly trees and shrubs may be aided by the heat bubble encompassing most cities. Marked alteration of the aeroallergen profile over time has been documented in some cities such as Tucson, Arizona and across the southwest with the introduction of crop trees such as olive.²¹

Table 3
Thommen's Postulates on pollen causation of hay fever^a

Pollen must contain an excitant of hay fever
Pollen must be anemophilous, or wind borne
Pollen must be produced in sufficiently large quantities
Pollen must be sufficiently buoyant to be carried considerable distances
The plant producing the pollen must be widely and abundantly distributed

^aThommen.¹⁰

Respirable Allergenic Particles

It has been noted that ragweed hay fever symptoms can persist for days after intact airborne pollen is no longer detectable, and this observation has spurred studies demonstrating aeroallergens in submicron particles, believed to be from fragmented pollen

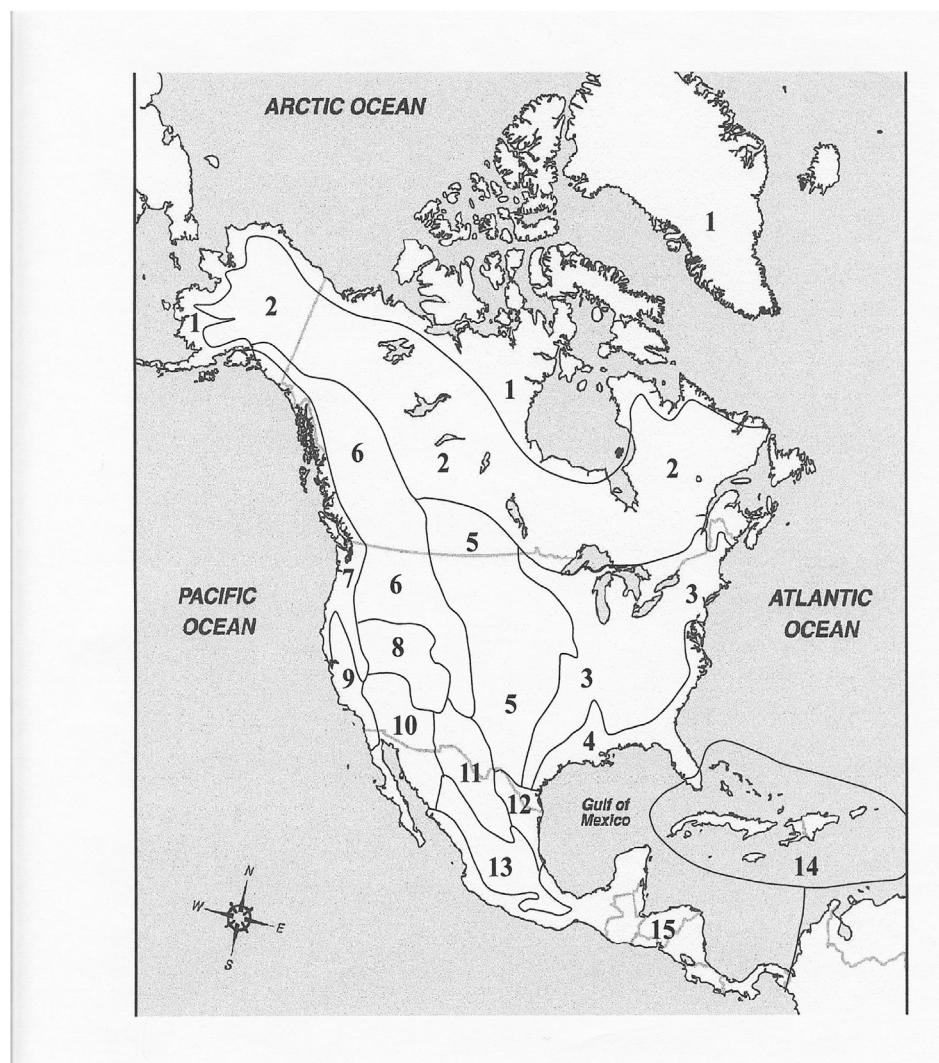


Figure 1. Modified version of the system developed by Takhtajan¹⁷ who divided North America into 5 regions containing 13 provinces or zones and then divided several of these provinces into subprovinces or sectors, resulting in 20 zones.

grains.^{22,23} Allergenic birch activity also has been demonstrated on airborne particles smaller than $2.4 \mu\text{m}$.²⁴ Starch granules are prominent in the cytoplasm of certain pollens such as the grasses (Poaceae) and docks (*Rumex*, Polygonaceae).²⁵ Such grass starch granules have heavy concentrations of major allergen groups 1, 5,

and 13.^{26–28} The force of storm-driven raindrops may disrupt pollen grains, releasing large amounts of respirable allergenic particles. Taylor et al²⁹ demonstrated that a moisture-drying cycle of grass pollen will result in starch granules emanating through the aperture or as a result of fragmentation of the grain.

Table 4
Impact of environmental factors on plants and allergens

Plant/pollen type	Environmental variable	Region	Impact	Reference
385 plant species	increased temperature	United Kingdom	onset flowering advanced average 4.5 d over decade; ~65 species advanced 15 d	42
Grass	increased temperature	Switzerland, Spain	increased counts, delayed onset, shorter season, lower counts	43,49
Birch	increased temperature	Switzerland, Denmark, Italy, United Kingdom	increased pollen counts, earlier season onset, higher peak level	43,44
Hazel	increased temperature	Switzerland	increased counts	43
Oak	increased temperature	Spain	earlier season onset	45
Alder	increased temperature	Spain	delayed onset 2–8 d	48
Olive	increased temperature	Spain, Italy	earlier onset and longer season, higher counts	46,47
Cypress	increased temperature	Italy	earlier onset and longer season, higher counts	47
Pellitory, <i>Parietaria</i> species	increased temperature	Italy	earlier onset, longer season, higher counts	47
Ragweed, <i>Ambrosia</i> species	increased temperature, increased CO ₂	Canada, United States, Poland	increased counts, earlier onset, longer season, increased range, increased biomass	52–56
Sagebrush, <i>Artemisia</i> species	increased temperature, increased CO ₂	Poland, United States	earlier season onset, increased biomass, increased ground cover	50,51

Meteorologic Variables

The impact of climate and weather on pollen concentration in the atmosphere is significant. Although prevalent weather helps define climate, individual weather conditions, such as rain, humidity, wind speed and direction, temperature, or amount of sunshine, will have indirect and direct effects on aeroallergens.^{30,31} Numerous studies from around the globe have tabulated regional pollen counts, and some have correlated counts with meteorologic variables. With the exception of temperature, humidity, and precipitation, there are no consistent correlations with many of these factors. The reason is the complexity of interactions between variables. From year to year, different variables are likely to play a central role in determining pollen counts. Weather conditions can have immediate effects, such as cleansing of the air of particulates with rain (“scrubbing effect”), or delayed effects, such as the accumulated cold followed by warmth necessary to induce flowering.

Rainfall will clean the air with the entrapment of pollen grains or mold spores by raindrops. McDonald³² reported that the efficiency of pollen capture depends less on the size of the grain than on the duration of rainfall and the character of the droplet. A light shower of 0.1-cm accumulated rainfall will be 99% effective in removing pollen if raindrops are drizzle size (approximately 0.2 mm) and only 75% efficient with larger 1.0-mm droplets. A thunderstorm flurry of large 4.0-mm drops will remove only 25% to 33% of the grains. Sustained rainfall of at least 1.0 cm will be 80% to 99% effective regardless of droplet size. Numerous reports have shown that increased humidity is associated with decreased pollen counts.³³ Grass anthers close with increased humidity, limiting pollen release during moist situations.²⁹ With drying, anthers reopen; similar observations have been made with other plants.

Thunderstorms have been linked to dramatic epidemics of asthma urgent care visits. In Calgary, Canada, during a midsummer 2-day interval in 2000, there was a near 10-fold increase in asthmatic urgent care complaints associated with a thunderstorm attributed to a sudden increase in pollen and spore counts.³⁴ In England, severe thunderstorms were associated with increased emergency visits in pediatric and adult patients with asthma, usually after high grass pollen counts.³⁵ Thunderstorm-induced asthma flares have been associated with increases in the grass pollen count.^{36–38} This may be due to resuspension of settled grains from the wind, the concentration of grains low to the ground owing to thunderstorm cell outflow bands, and increased airborne grass allergens on starch granules from disrupted grains.³⁹

Impact of Climate Change on Aeroallergens

Reviews by Beggs⁴⁰ and Shea et al⁴¹ showed a wealth of evidence for the impact of climate change on allergenic plants. Numerous studies have shown earlier onset and longer season, greater total counts, and higher peaks.^{42–47} However, northern trees such as the alder have been delayed because of insufficient cold accumulation necessary for breaking dormancy, and 1 study from Spain showed delayed grass season onset.^{48,49}

Artemisia frigida is a mat-forming, short, perennial shrub and is the most widespread and abundant *Artemisia* species in the world. Experimentally doubling CO₂ over ambient levels on Colorado short-grass steppe plots showed a 40-fold biomass and a 20-fold percentage ground cover increase of *A. frigida*.⁵⁰ The *Artemisia* pollen season has advanced in Poland.⁵¹

Experimental manipulation of CO₂ and temperature has resulted in the greater biomass and pollen production of short ragweed.^{52–54} Using the urban environment as a surrogate for climate change, Ziska et al⁵⁵ showed greater above-ground biomass, earlier flowering, and more pollen production in an urban compared with a rural site. Ragweed season lengthening has been demonstrated in more northerly latitudes because of delayed

first frost.⁵⁶ Table 4 delineates environmental factors and their impact on aeroallergenic plants.

Conclusions

Seed plants have evolved during the past 400 million years. Gymnosperms were the first to be pollinated by wind, whereas angiosperms initially evolved vector-assisted pollination in concordance with the evolution of the vectors. Wind pollination has survival benefit in regions where vectors are scarce. Anemophilous plants frequently have floral modifications separating male and female structures. Floristic zones are determined by multiple physical factors and are characterized by the endemic flora. Meteorologic variables have had a long-term impact on defining floristic zones, delayed effects on flowering onset, and shown immediate effects on airborne pollen levels. Shifts in CO₂ and temperature have affected the production and timing of airborne allergens, resulting in increasing aeroallergen exposure.

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