

Changing Pollen Types/Concentrations/ Distribution in the United States: Fact or Fiction?

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The buildup of greenhouse gases in the atmosphere has resulted in global climate change that is having a significant effect on many allergenic plants through increases in plant productivity and pollen allergenicity and shifts in plant phenology. Based on experimental studies, increased atmospheric levels of carbon dioxide have directly increased plant productivity. This has affected the total amount of pollen produced in some species. Research has also shown increased levels of birch allergen at warmer temperatures. Warmer temperatures have resulted in earlier flowering for many spring-flowering species in many countries, recorded through visual observations of flowering and by airborne pollen. Increases in the cumulative season totals of various pollen types also have been recorded; some of these increases may be explained by changes in plant distribution.

Introduction

During the past 200 years, human activities such as the burning of fossil fuels have produced increases in greenhouse gases in the atmosphere; the buildup of these heat-trapping gases has resulted in changes to the global climate, especially increasing global temperature [1]. The direct and indirect effects of these changes may involve ecosystem disturbance, sea level rise, changes in the distribution of plants and animals, and changes in plant productivity and phenology (the timing of developmental stages). Changes in productivity are directly related to the enriching effects of increased carbon dioxide on rates of photosynthesis. Changes in plant phenology are related to the warmer spring temperatures and considered a sensitive, easily observable measure of climate change. Data from

Europe and North America show earlier flowering and first leaf appearance for many plant species. Although many of these studies are focused on plants (eg, lilac) with insect-pollinated flowers, other studies also show earlier flowering in anemophilous, wind-dispersed species.

Other significant consequences of climate change concern human health and increased incidence of plant and animal diseases [2]. Direct effects on human health include deaths due to extreme weather events (eg, heat waves, hurricanes, and flooding). The spread of some infectious diseases is an indirect effect that can be linked to global warming, as the distributions of mosquitoes and other arthropod vectors have expanded. The severity of respiratory diseases such as asthma and allergic rhinitis also can be considered an indirect effect attributed to climate change because of changes in the concentrations of airborne pollen and spores [2].

Many excellent review articles address various aspects of global climate change [1,3]. The present review addresses some of the evidence of global climate change and emphasizes the recent literature showing changes in aeroallergen exposure that result from shifts in plant productivity, allergenicity, and phenology.

Global Climate Change

The anthropogenic emission of greenhouse gases is increasingly recognized as a significant contributor to the rise of average global temperatures and climate change [1]. Natural greenhouse gases (carbon dioxide, methane, and nitrous oxide) have risen substantially since the beginning of industrialization in the mid-1700s. Carbon dioxide has trended upward exponentially from preindustrial levels of approximately 280 ppm [1] to the current average global level (November 2007) of 384 ppm [4]. Methane has risen from a relatively stable preindustrial value of approximately 700 parts per billion (ppb) to its 2005 value of 1774 ppb [5]. Nitrous oxides have also risen from 314 ppb to 319 ppb (1998–2005), much higher than the average value of 180 to 260 ppb found in longer geologic records covering the last glacial to interglacial cycle. Synthetic greenhouse gases

(chlorofluorocarbons, hydrofluorocarbons, perfluorocarbons, halons, and sulfur hexafluoride) also contribute to warming, although most of these are declining because of restrictions imposed by the Montreal Protocol to protect upper atmospheric ozone. Models of carbon dioxide use project increases in atmospheric carbon dioxide levels above 500 ppm before the beginning of the next century [6]. This increase presents the clearest potential for and danger of continued changes to global climate.

Increases in greenhouse gases have concurred with the rise of the estimated global mean surface temperatures by $0.74^{\circ}\text{C} \pm 0.18^{\circ}\text{C}$ over the last century (1906–2005). However, the trend is not linear. During the past 50 years, temperatures have increased $0.76^{\circ}\text{C} \pm 0.19^{\circ}\text{C}$ more than the first 50 years of instrumental records (1850–1899) [7]. Also, the rate of warming over the past 50 years is almost double the rate over the past 100 years. Beyond the global average temperature rise, daily and seasonal temperature ranges continue to show high levels of spatial variability. For example, the overall increase in maximum temperatures was greater than increased minimum temperatures from 1950 to 2004, resulting in a declining diurnal temperature range. Since then, the diurnal temperature range has remained nearly constant, as minimum and maximum temperatures have risen simultaneously [8]. With this increase in temperatures has come an overall reduction in the number of frost days at the mid-latitudes.

Changes in extreme temperatures are also noted, with observed extreme cold conditions becoming more rare from 1951 to 2003 and warm nights more frequent. However, stochastic variability continues to impact vegetation, as short, sharp temperature fluctuations below freezing remain. Coupled with temperature changes are increased levels of precipitation at the higher northern latitudes and significant reductions in rainfall within the deep tropics. Precipitation patterns are more spatially and temporally heterogeneous compared with temperatures. However, individual heavy precipitation events appear to be more common in areas of increased and decreased total precipitation amounts, an observation consistent with an overall rise in water vapor levels around the globe [9]. At the same time, a marked increase in the severity, duration, and aerial extent of drought conditions and heat waves and the reduction of soil moisture have been recorded regionally.

Changes in Plant Productivity

Increased atmospheric carbon dioxide is one of the most important drivers of climate change. Carbon dioxide also directly affects carbon availability for plants as the primary carbon resource obtained through photosynthesis. The temperature increases resulting from the accumulation of greenhouse gases also may affect plant productivity and development. Over the past two decades, experiments have been undertaken to determine the projected effects of increasing atmospheric carbon dioxide on plants and

ecosystems. These have included greenhouse experiments, the use of indoor and outdoor growth chambers, and the study of entire ecosystems using Free Air Carbon Dioxide Enrichment experiments [10]. The resulting data were produced using a wide range of experimental designs and, therefore, have become increasingly difficult to synthesize. Researchers have increasingly turned to meta-analyses to provide quantitative summaries and generate higher-order conclusions from the wide variety of experimental designs and data [10–12].

Studies in response to increasing carbon dioxide

Research shows that increasing atmospheric carbon dioxide by about 200 ppm above ambient atmospheric levels (600 ppm), a near-doubling from historic, preindustrial levels of 280 ppm, increases photosynthesis by as much as 60% in some C_3 plant species [11,13]. This shift in carbon acquisition has predicted direct and indirect effects on plant physiology, such as shifts in species biogeographic distribution, phenology, and reproductive behavior.

The impact of increasing atmospheric carbon dioxide on plant systems and potential allergen production focuses on increased plant biomass, flower production, and pollen. A natural split occurs within the literature between crop plants and wild species, with a further differentiation between physiologic types based on photosynthesis (C_3 legumes, C_3 , and C_4 physiology). Jablonski et al. [12] analyzed 1391 pairs of observations from 159 reports on 79 crop (75%) and wild (25%) species reported between 1983 and 2000. Their meta-analysis was designed to assess the effects of carbon dioxide enrichment (500–800 ppm) on reproductive organs, including plant biomass, flower number and carbon allocation between plant mass, and reproduction. Within all plant types, total plant mass increased by 31% in elevated carbon dioxide compared with controls, with the greatest response in C_3 legumes, then C_3 , and then C_4 plants. Significantly greater flower production (+ 19%) occurred, with no significant differences between crop and wild species or when species were split into physiologic categories of C_3 legumes, C_3 , and C_4 plants. Overall reproduction allocation was not significantly different between ambient and raised carbon dioxide levels. The only categorical difference was between crop and wild plants, with crop plants showing little change but high levels of variability and wild plants showing reduced reproduction allocation and variability. The increase in flower number is consistent with the findings of Kimball [14], who compiled 430 historic experimental observations of 37 agricultural species grown under enriched atmospheric carbon dioxide conditions. These historic studies show a 33% increase in crop yield measured as changes in crop plant biomass by weight. However, the species analyzed included a subcategory of species raised specifically for their flowers. These floral crops (carnation, chrysanthemum, cyclamen, nasturtium, rose, and snapdragons) showed a significant

increase in flower production, with the implication being that increasing carbon dioxide produces more flowers. The frequent use of carbon dioxide burners in commercial greenhouses to boost floral production is further evidence of this phenomenon.

Studies of pollen production at elevated CO₂ levels

Increases in biomass and, subsequently, greater numbers of flower heads are expected to increase pollen production. Rogers et al. [15••] grew three cohorts of *Ambrosia artemisiifolia* separated by 15-day increments at ambient and carbon dioxide concentrations of 700 ppm. At heightened carbon dioxide levels, plants from the two later cohorts had greater biomass and overall increased pollen production of 32% and 55%, respectively. Initial cohorts showed similar values with both treatments. Higher pollen production levels also occurred in subordinate versus dominant plants in dense stands with increased carbon dioxide levels. Ziska et al. [16,17] reported similar results of increases in flower heads along with overall plant biomass in *A. artemisiifolia*. Elevated levels of carbon dioxide increased the number of floral spikes per plant. In addition, an overall increase in the number of pollen grains per spike increased, resulting in increased pollen production as measured by grams of pollen per plant. However, it is unclear if there were any changes in the number of pollen grains per flower. From preindustrial carbon dioxide levels to current levels and from current levels to 600 ppm, the number of flower spikes per plant remained steady but increased significantly from current to future carbon dioxide levels. However, pollen production increased initially and then held steady as future carbon dioxide levels were applied. Overall, the change from historic to ambient levels increased pollen production by 132%, and the shift from ambient to 600 ppm increased production by approximately 90%. Wayne et al. [18] found similar but overall reduced pollen production levels (+ 61%) with heightened carbon dioxide concentrations of 350 ppm to 700 ppm. Some caution must be exercised in interpreting these results. Prasad et al. [19] and Koti et al. [20] found the normally high pollen production values significantly decreased in kidney beans (*Phaseolus vulgaris*) and soybeans (*Glycine max*) when they were grown with higher temperatures. Koti et al. [20] found similar results for high UVB concentrations. These studies show that other environmental variables may mitigate some of the increases observed with only increasing carbon dioxide levels.

A significant portion of allergenic pollen is produced by larger perennial plants, shrubs, and trees. These large plants are harder to study, as their size and the time needed to reach fecundity necessitate a significant investment to realize results. Curtis and Wang [11] reviewed 508 observations of the effects of heightened carbon dioxide on woody plant biomass accumulation taken from 79 reports and 59 species. Results indicated a significant increase in biomass with high carbon dioxide levels (28%). However, stress

effects significantly reduced overall gains. For example, plants grown under nutrient stress showed about half of the average gains (+ 15.5%) compared with plants without stress (+ 30.9%). In the Duke forest Free Air Carbon Dioxide Enrichment experiment [21], *Pinus taeda* was grown at ambient and ambient-plus-200-ppm carbon dioxide concentrations [22,23]. After more than 5 years of growth at heightened carbon dioxide concentrations, the proportion of trees reaching fecundity was greater, the diameter of the fecund trees smaller, and the overall number of male and female cones and seeds increased. In the male cones, the absolute amount of pollen per cone was not altered. However, with greater cone numbers and earlier fecundity, this led to increased stand-level pollen production [23].

Another potential impact of global change and allergenic particles occurs when developmental changes within individual pollen grains heighten their allergenicity. For example, birch (*Betula pubescens* subsp. *czerepanovii*) growing at different temperatures showed an increase in the major allergen protein Bet v 1 at higher temperatures [24]. These results are supported by earlier work that showed increased allergenicity in pollen from the warmer southern side of individual *B. pubescens* trees [25]. Changes in secondary plant products with heightened carbon dioxide, such as allergens, are not unprecedented. For example, poison ivy (*Toxicodendron radicans*) grown at high levels of atmospheric carbon dioxide exhibits changes in secondary plant products. Plants grown at twice current ambient conditions (570-ppm carbon dioxide) show increased production of and a more allergenic form of urushiol, the cause of contact dermatitis [26].

Studies of flowering in response to warming

In contrast to the previous studies, which examined plant responses to increased carbon dioxide levels, several researchers have examined responses to experimental warming in field plots. Wan et al. [27] examined the responses of *Ambrosia psilostachya* (western ragweed) in a tallgrass prairie to experimental warming over 2 years and found that warming increased the number of ragweed stems in the plot by 88%. Warming caused no change in the pollen production per stem, but total pollen per plot increased by 84% because of the increased number of stems. Sherry et al. [28••] showed the effects of experimental warming on flowering in a variety of species from another tallgrass prairie site. They found advanced flowering in species that flower in spring and early summer but delayed flowering in species that normally flower in late summer and fall. Nine spring-flowering species showed earlier flowering. Two summer-flowering grasses showed a significant change in flowering time. *Panicum* spp flowered 17 days earlier, and *Andropogon* spp flowered 10 days later. *Ambrosia* spp plants emerged earlier than unwarmed plants, developed buds at the same time, but flowered later in the warmed plots. The authors concluded that the delayed flowering for *Ambrosia* spp was due to a prolongation of the bud stage.

Plant Phenology

Plants and animals in temperate zones display seasonal changes that are synchronized to climate. Phenology is the scientific discipline that studies these changes and includes investigations of phenomena such as the appearance of the first leaves, first flowers, autumn leaf coloration, animal migration, and onset of egg laying by birds and other animals. Although researchers have reported on phenologic observations for centuries [29], the recent interest in global climate change has imparted a renewed emphasis on documenting these events [30]. In this review, we confine our discussion to flowering phenology.

It has long been recognized that reproductive phenology in many plants is more closely related to temperature than other environmental factors [31]. This is especially true for plants that flower in spring and early summer, whereas species that flower in late summer and fall generally are correlated with photoperiod. Flowering in spring is largely a response to accumulated temperature above a specific threshold value; therefore, years with warmer springs show earlier flowering [32]. In addition to year-to-year fluctuations of spring temperatures, increases in global temperature have resulted in warmer winters and springs and, consequently, earlier flowering of many spring taxa in various locations [33,34,35••]. Although a few studies have shown an extension of the flowering period for some species that bloom in fall [28••], most phenologic reports have focused on shifts in spring flowering.

Visual observations of flowering

Long-term phenologic databases for flowering are often based on visual observation at a single location or multiple locations. Typically, the date of first bloom is recorded, although some studies have used other metrics. Fitter and Fitter [33] reported on the first flowering date for 385 species over a period of 47 years. One of the authors recorded all the observations from a single location. From 1991 to 2000, the dates of first flowering were on average 4.5 days earlier than those from 1954 to 1990. Sixty species from this group had significantly earlier flowering (at least 15 days in advance). Also, insect-pollinated species showed a greater change than wind-pollinated ones (4.8 vs 3.5 days earlier).

Menzel [30] reported on observational data obtained from the International Phenology Gardens, a network of gardens in Europe that has genetically identical trees and shrubs. Many of the trees in the gardens are of allergenic importance, including *Betula*, *Populus*, *Quercus*, and *Salix* spp. Data for 16 taxa from 1959 to 1996 showed trends for earlier flowering, although different countries varied in regard to the species showing this trend. Overall, the data indicated that spring phenologic events advanced 6.3 days during the period of study. Menzel et al. [34] published a Europe-wide meta-analysis of all recorded changes in phenology from 1971 to 2000 for 542 species in 21 countries. The datasets analyzed consisted of more than 100,000 phenologic time series. Their results showed that 78% of all

leaf unfolding and flowering records were advanced, with 31% significantly advanced. Overall, the average advance in spring phenology was 2.5 days per decade. The authors concluded that the spring phenologic signal is an excellent indicator of the impact of climate change.

Plant phenology data for North America are not as widely available as European datasets. Fewer species have been studied and for shorter periods of time. The lilac (*Syringa vulgaris* and *Syringa chinensis*) and honeysuckle (*Lonicera tatarica* and *Lonicera korolkowii*) databases are the longest in the Western Hemisphere. Regional plantings of these species were established in the late-1950s and 1960s to develop phenologic datasets that could be used to optimize farming practices [36]. These species were chosen because they can grow in many soil types and geographical areas and under various climatic conditions [37]. Phenology data from these plants have been analyzed in various studies. Schwartz and Reiter [38] examined lilac flowering data from 1959 to 1993 and found regional differences in North America along with a 4.2-day advance in first bloom date. First bloom dates for lilac (1957–1994) and honeysuckle (1968–1994) from 12 western states showed extensive variability among states and from year to year [37]. For example, the average first bloom date for lilac ranged from mid-March in Arizona to early-June in Montana and Washington. Overall, there was a trend toward earlier flowering for lilac and honeysuckle since the mid-1970s. For lilac, flowering was advanced 7.5 days over 38 years, and honeysuckle 10 days over 27 years. Wolfe et al. [36] examined lilac first flower date from 1965 to 2001 in the northeastern United States along with midbloom dates for apple (*Malus domestica*) and grape (*Vitis vinifera*). Earlier flowering was found in most lilac locations, with an average of 9.3 days over the 36-year period. Although the datasets for apple and grape had very few locations, these species showed a 5- to 7-day earlier midbloom date.

In western Canada, Beaubien and Freeland [32] examined changes in flowering using historical and modern phenologic datasets. They found a linear trend toward earlier flowering in aspen (*Populus tremuloides*) trees, with an advance of 26 days from 1900 to 1997.

Several investigators used specimens in large herbaria and historical observations to determine flowering dates as a surrogate for long phenologic observations. Primack et al. [39] used herbarium specimens in Arnold Arboretum in Boston to compare flowering times from 1885 to 2002. They found that plants flowered 8 days earlier from 1980 to 2002 than they did from 1900 to 1920. Miller-Rushing and Primack [40] analyzed 500 taxa growing in Concord, Massachusetts. Observations were taken by Henry David Thoreau from 1852 to 1858, then by Alfred Hosmer in 1878 and 1888 to 1902, and finally by the authors from 2004 to 2006. Analysis showed spring-flowering plants advanced on average 7 days earlier. Over the same period, summer-flowering species showed greater interannual variation; the overall

correlation of summer-flowering species with temperature was less than it was for spring-flowering taxa.

Airborne pollen

Data from airborne pollen levels also have been used as evidence of earlier flowering in select taxa, although pollen databases generally are not as long as the records of visual observations. Various studies have examined several pollen season parameters, including start date, peak date, peak values, total seasonal pollen, and length of pollen season. Most of these studies have been conducted in Europe because of the availability of longer aerobiologic databases.

Birch (*Betula* spp) pollen is a major aeroallergen in many European countries; consequently, many studies have focused on changes in airborne birch pollen concentrations. Rasmussen [41] examined birch pollen from two cities in Denmark and documented several changes from 1979 to 1998. The season start date became significantly earlier in Copenhagen by 12 days and in Viborg by 10 days. The peak date for the birch season was also earlier in both cities. During those 20 years, there was a significant increase in total pollen levels for the season and increases in the peak values. Emberlin et al. [42] investigated trends in the start of the *Betula* spp pollen season at several sites in Europe, including Kevo, Turku, London, Brussels, Zurich, and Vienna. The authors compared birch pollen data from 1982 to 1999, although longer datasets were used for some sites. They found marked regional differences in the birch seasons. London, Brussels, Zurich, and Vienna showed clear trends toward earlier start dates. By contrast, Kevo, located within the Arctic Circle in northern Finland, showed a trend toward cooler springs and, consequently, later start dates during this period. Turku (southern Finland) showed fluctuating temperatures in spring and no clear long-term trends for the start of the *Betula* spp season. Van Vliet et al. [43] showed that the start date for birch pollen in Leiden (the Netherlands) was significantly earlier (by 10 days) from 1969 to 2000. In another multicity study in western Europe, Spiekma et al. [44] investigated the cumulative annual totals of several pollen types, including *Betula* spp. The datasets vary from 20 to 33 years in five cities, and increasing trends for total birch pollen were noted at all sampling stations. The trends from Delmenhorst (Germany), Helmond (the Netherlands), and Brussels were not significant; however, Derby (United Kingdom) and Leiden had significant increases in annual totals over 32 and 33 years, respectively.

European researchers also have found significant trends over time for other airborne pollen types. Earlier season starts have been documented for *Juniperus*, *Ulmus*, *Populus*, *Salix*, and *Quercus* spp in the Netherlands [43] and for *Platanus* spp pollen in Spain and Italy [45]. Spiekma et al. [44] found significant increases in annual pollen totals for *Urtica* spp pollen at Delmenhorst, Helmond, Brussels, Leiden, and Derby and for *Quercus* spp pollen at Brussels, Leiden, and Derby.

The air-sampling datasets at several European cities extend back to the late-1960s; very few US sampling stations have been in continuous operation for that long. Although newspaper stories and anecdotal reports based on 2 or 3 years of data have described earlier start dates and increased pollen levels, long-term datasets are needed to rule out changes due to year-to-year fluctuations in weather conditions. As more sampling stations maintain yearly pollen records, data for the United States should become available in the future.

Daily aerobiology data from Tulsa, Oklahoma, extend back to 1987 using a Burkard sampler and show several long-term trends in airborne pollen levels. Levetin [46] reported significant increases in cumulative season totals of *Juniperus*, *Quercus*, *Carya*, and *Betula* spp pollen from 1987 through 2000 and also found earlier but non-significant start dates for *Juniperus*, *Ulmus*, and *Morus* spp pollen. Perhaps the most important change in the Tulsa pollen record has been the increase in *Juniperus* spp pollen totals, which continued to show a significant increase in cumulative season totals ($r = 0.61$, $P < 0.005$) from 1987 to 2006 [47].

The *Juniperus* spp pollen increase registered in Tulsa paralleled increases in *Juniperus virginiana* trees throughout Oklahoma and other states in the Central Plains over the past several decades [48]. Similar increases have been documented with other *Juniperus* spp in the central, western, and southwestern US; this includes the highly allergenic species *Juniperus ashei* [49]. Various theories have been proposed to explain the expansion of *Juniperus* spp populations, including fire suppression, overgrazing, and climate change. Knapp and Soulé [50] examined the expansion of *Juniperus occidentalis* populations in central Oregon and suggested many environmental factors, including carbon dioxide increase, have contributed to the population change. The carbon dioxide increase preferentially enhanced the growth of young *J. occidentalis* trees [50].

Cumulative *Ambrosia* spp pollen totals in the Tulsa atmosphere showed a significant decrease ($r = -0.78$, $P < 0.001$) during this same period (1987–2006) [51]. Although increased urbanization may contribute to the decrease in ragweed pollen totals, analysis of meteorologic factors showed that increasing August temperature was a significant negative variable. These data are somewhat in contrast to those of Wan et al. [27], who showed that experimental warming increased the number of *A. psilostachya* stems per plot and, consequently, the total pollen per plot. *A. artemisiifolia* and *Ambrosia trifida*, the most common ragweed species in the Tulsa area, are annuals. It is possible that the perennial ragweed *A. psilostachya* responds differently than the annuals.

Conclusions

Elevated levels of atmospheric carbon dioxide and other greenhouse gases have resulted in global warming. The

effect of these changes has impacted plant production, with increases in plant biomass, numbers of flowers, pollen per plant, and potential changes in pollen per anther. These effects have been shown in select plants through studies at elevated carbon dioxide levels. The timing of floral development and pollen release depends upon environmental signals, especially temperature for spring-flowering species, and as a result of global climate change, these natural cycles potentially may be disrupted by shifts in climate that result in an advance in the timing of pollen development and dispersal. Data from European studies have documented these changes in phenology through visual observations of flowering and airborne pollen. Increases in peak concentrations and cumulative annual pollen levels also have been recorded. Parallel changes are occurring in the United States, although the databases for both measurements are not as extensive. The most widely documented changes in plant distribution and, consequently, pollen levels are the expansion of *Juniperus* spp across the Central Plains and southwestern and western United States. Although the reasons for the expansion are complex and not fully understood, changing carbon dioxide levels may be a contributing factor. Continued pollen monitoring in the United States is essential to document these and other future pollen trends related to climate change.

Disclosures

No potential conflicts of interest relevant to this article were reported.

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