Rising CO_2 and pollen production of common ragweed (*Ambrosia artemisiifolia*), a known allergy-inducing species: implications for public health

Lewis H. Ziska[A] *and Frances A. Caulfield*

Climate Stress Laboratory, Bldg 046A, USDA-ARS, Beltsville Agricultural Research Center, 10300 Baltimore Avenue, Beltsville MD 20705, USA.
[A]Corresponding author: email; ziskal@ba.ars.usda.gov

Abstract. Although environmental factors such as precipitation and temperature are recognized as influencing pollen production, the impact of rising atmospheric carbon dioxide concentration ($[CO_2]$) on the potential growth and pollen production of hay-fever-inducing plants is unknown. Here we present measurements of growth and pollen production of common ragweed (*Ambrosia artemisiifolia* L.) from pre-industrial $[CO_2]$ (280 μmol mol^{-1}) to current concentrations (370 μmol mol^{-1}) to a projected 21st century concentration (600 μmol mol^{-1}). We found that exposure to current and elevated $[CO_2]$ increased ragweed pollen production by 131 and 320%, respectively, compared to plants grown at pre-industrial $[CO_2]$. The observed stimulations of pollen production from the pre-industrial $[CO_2]$ were due to an increase in the number (at 370 μmol mol^{-1}) and number and size (at 600 μmol mol^{-1}) of floral spikes. Overall, floral weight as a percentage of total plant weight decreased (from 21% to 13%), while investment in pollen increased (from 3.6 to 6%) between 280 and 600 μmol mol^{-1} CO_2. Our results suggest that the continuing increase in atmospheric $[CO_2]$ could directly influence public health by stimulating the growth and pollen production of allergy-inducing species such as ragweed.

Keywords: allergens, elevated carbon dioxide, photosynthesis, pollen, relative growth rate.

Introduction

Since the start of the Industrial Revolution, atmospheric $[CO_2]$ has risen from ~280 μmol mol^{-1} to ~370 μmol mol^{-1} (Houghton *et al.* 1996). This rise in atmospheric $[CO_2]$ has not been linear. Approximately two-thirds of the observed increase in $[CO_2]$ has occurred since the 1950s (Keeling and Whorf 1994). Although the projected rate of future atmospheric $[CO_2]$ increase varies by model, it is generally acknowledged that atmospheric $[CO_2]$ should reach 600 μmol mol^{-1} sometime during the 21st century (Houghton *et al.* 1996).

Because CO_2 supplies the carbon for all terrestrial biology, research efforts have focused on determining the impact of rising atmospheric $[CO_2]$ on the growth and reproduction of native species and crops (e.g. Kimball *et al.* 1993; Poorter 1993; Curtis and Wang 1998). Reproduction is an especially important parameter since it affects both ecological fitness for native species, and economic production for crops.

The impact of $[CO_2]$ on allocation of resources to flowering and changes in reproductive phenology appears to be highly species-specific (Ackerly and Bazzaz 1995). Enhanced $[CO_2]$ has resulted in earlier flowering (Lawlor and Mitchell 1991) and increased flower and fruit number for a number of agronomic plants (Deng and Woodward 1998). In contrast, flowering of some native species has been unaffected or delayed with increased $[CO_2]$ (Garbutt and Bazzaz 1984; Reekie *et al.* 1997), but this is by no means a universal response (e.g. *Datura stramonium*, Garbutt and Bazzaz 1984).

While specific attention has been given to aspects of reproductive biology which could influence seed development and yield, almost nothing is known concerning the impact of $[CO_2]$ on pollen production *per se*. Aside from the obvious consequences for fertilization, fecundity and ecological fitness, $[CO_2]$-induced changes in pollen production could have a direct impact on atmospheric pollen concentration, with subsequent effects on human allergic disease and public health. For example, in a recent survey among the general population in the US, approximately 70% of respondents indicated pollen as the principal agent producing symptoms of allergies, with ragweed pollen cited as the individual plant species eliciting the greatest response (Meggs *et al.* 1996). In addition to ragweed, other weedy species (e.g. lambsquarters, *Chenopodium album* L.) and pigweed (*Amaranthus retroflexus* L.) as well as native trees

Abbreviations used: A, rate of CO_2 assimilation; C_a, ambient CO_2 concentration; C_i, internal CO_2 concentration; DAS, days after sowing; PPFD, photosynthetic photon flux density; RGR, relative growth rate.

10.1071/PP00032 0310-7841/00/100893

(e.g. *Quercus* and *Acer* spp.) and grasses (e.g. *Setaria*) are recognized as influencing seasonal allergies through pollen production (Gergen and Turkeltaub 1992; Emberlin 1994).

In the current experiment, our principal objective was to test whether the increase in atmospheric [CO_2] since the Industrial Revolution, and projected future increases in [CO_2], may alter growth and pollen production of known hay-fever-inducing plants using common ragweed (*Ambrosia artemisiifolia* L.) as a model species. Pollen production of ragweed is generally acknowledged to be a major source of air-borne allergens and a public health concern in North America. In general, ragweed production peaks between late August and November in North America, and is the principal pollen associated with fall allergies in the US (Frenz *et al.* 1995; Meggs *et al.* 1996). CO_2-induced changes in the life cycle and pollen-producing capacity of aero-allergen plants such as ragweed could have significant implications for public health.

Materials and methods

Experiments were conducted using a controlled environment chamber located at the Climate Stress Laboratory, USDA-ARS, Beltsville, MD, USA. An environmental chamber was used rather than field chambers or Free-Air CO_2 Exchange (FACE), in order to maintain constant pre-industrial [CO_2] at a given temperature and consistent light and humidity for 24-h periods.

[CO_2] was controlled by flushing the chamber with CO_2-free air using a Ballston 75-60 type CO_2 scrubber (Ballston Filter Products, Lexington, MA, USA), then re-injecting CO_2 to the desired [CO_2]. Injection of CO_2 was controlled by an infrared gas analyser (WMA-2, PP systems, Haverhill, MA, USA) in absolute mode that sampled chamber air continuously. The set points for [CO_2] control were 280 (pre-industrial), 370 (current) and 600 (future) μmol mol^{-1} CO_2. Actual CO_2 concentrations determined at 10-min intervals over 24 h for each [CO_2] treatment were 281.5 ± 23.4, 374 ± 14.1 and 603 ± 12.9 μmol mol^{-1}, respectively. In all chambers, plants received 14 h of 1.0 mmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD) from a mixture of high-pressure sodium and metal halide lamps for the first 35 days after sowing (DAS). After 35 DAS, PPFD was altered to 12 h of 1.0 mmol m^{-2} s^{-1} PPFD to induce flowering. Day/night temperature was 28/22°C and average daily humidity exceeded 60%. Temperature, [CO_2] and relative humidity were monitored and recorded at 1-min intervals by an EGC network data logger (EGC Corp., Chagrin Falls, OH, USA) in conjunction with a PC.

Seeds of common ragweed (*Ambrosia artemisiifolia* L.) were broadcast in pots of different sizes ranging from 10 to 30 cm in diameter (1.8–21.2 L in volume). Smaller pots were elevated so that the height of the plants was uniform. Seed was obtained from the Valley Seed Company (Fresno, CA, USA). Plants in all pots were thinned to one plant per pot within 48 h after emergence. Pots were filled with vermiculite and watered daily to dripping point with a complete nutrient solution containing 13.5 mM nitrogen (Robinson 1984). For each experiment, 32 pots were assigned to a given [CO_2], with pots arranged to avoid mutual shading.

To determine potential changes in photosynthesis as a function of the growth [CO_2], single leaf photosynthesis (A, the rate of CO_2 assimilation) was determined as a function of short-term changes in internal [CO_2] (C_i) twice during the vegetative growth at each [CO_2] treatment. Assimilation was determined on the uppermost, fully expanded leaf for four plants of each [CO_2] between 30 and 40 DAS using a differential infrared CO_2 analyser (model 6252, Li-Cor Corp., Lincoln, NE, USA) in an open configuration attached to two single-leaf cuvettes. Temperature, humidity and [CO_2] were set to approximate values maintained in the growth chamber. The gas stream was humidified by bubbling through a temperature-controlled water bath to obtain a given dew point, and humidity was monitored with a dew point hygrometer (Hygro M-1, General Eastern Corp., Cambridge, MA, USA). Mass flow controllers were used to mix dry CO_2-free air with 100% CO_2 to obtain a desired [CO_2] within a cuvette. Supplemental lighting was supplied by a 150-W cool-beam floodlight (GE Corp., Cleveland, OH, USA) attached to a variable transformer to obtain a desired PPFD.

Photosynthesis was determined initially as the CO_2 assimilation rate at the growth [CO_2] (C_a) at the growth PPFD (1.0 mmol m^{-2} s^{-1}), then re-measured at saturating light intensity (1.6 mmol m^{-2} s^{-1}). C_a was then reduced to 90 μmol mol^{-1} and increased in steps to 180, 360, 720, 1080 and 1450 μmol mol^{-1}. Sufficient time (usually 20–30 min) was given after C_a was changed, to allow equilibration. At the end of the measurement, leaf laminae contained within a cuvette were cut, and leaf area determined with a leaf area meter (Li-Cor Corp.).

For each [CO_2] treatment, six plants were harvested at 21, 25, 29 and 35 DAS and again at seed maturity. Seed maturity was defined as occurring when seed set exceeded 90%. At each harvest, all plants for a given [CO_2] treatment were cut at ground level and separated into leaf laminae, stems (including petioles) and roots. Smaller-volume pots were harvested first to avoid root-binding effects. Total leaf area was determined photometrically as described previously. Dry weights were obtained separately for leaves, stems and roots. Material was dried at 65°C for a minimum of 72 h or until dry weight was constant, and then weighed. For the maturity harvest, leaf area was estimated based on the regression analysis between leaf area and weight obtained from previous harvests ($R^2 = 0.99$).

Before pollination, 10 terminal staminate floral spikes (catkins) were selected on each of five plants from each [CO_2] treatment, and labeled. A 5 × 25 cm polyethylene bag was placed over each spike to collect pollen. Each bag had a 2.5-cm slit cut approximately 2 cm from the bottom of the bag, into which the floral spike was placed with the peduncle of the raceme located at the bottom of the slit. After placement of the bag, the slit was taped so the floral spike was inside the bag with at least 5 cm of space from the top of the open bag. Tops of bags were left open for air circulation and ventilation. Floral heads were tapped gently each day, and pollen was allowed to fall to the bottom of the bag. After flowers were dehiscent and heads had completed pollen production, each bagged floral spike was cut immediately below the first flower and the floral structure was removed from the bag after tapping any residual pollen. Each spike was measured for length along with fresh and dry weights. Total pollen for a given spike was calculated by subtracting the initial bag weight from the bag and pollen weight. At maturity, for each plant from each [CO_2] treatment, the total number of floral spikes was recorded, spikes were harvested and the dry weight (without pollen) recorded. The ratio of pollen collected to dry weight of the floral structure resulted in a consistent ratio that was used to estimate pollen production per plant.

Because of potential differences in microclimate between chambers, the same growth chamber was used for all three CO_2 levels. Adjustments to PPFD, humidity and temperature control were made prior to the start of each [CO_2] treatment to maintain consistency in microclimate. In addition, the entire experiment (i.e. all three [CO_2] treatments) was repeated. A two-way ANOVA (SuperANOVA, Abacus Concepts, Berkeley, CA, USA) was used to test for differences between the two runs and between treatments. Because no significant run effect was detected, treatment effects were compared with a one-way analysis of variance on the combined data. Final biomass for a given [CO_2] treatment differed by <10% between runs. Three separate post-hoc tests (Student–Newman–Keuls, Duncan New Multiple Range and Fisher's

protected LSD) determined differences at the 0.05 significance level as a function of [CO_2] treatment.

Results

Pollen production increased significantly with rising [CO_2]. The observed increase was 132% from pre-industrial to current CO_2 levels, and ~90% from current to future CO_2 levels of 600 μmol mol^{-1} (Fig. 1). Sensitivity of pollen production to increasing [CO_2] was greater from pre-industrial to current CO_2 levels (0.7 g of pollen per 10 μmol mol^{-1} increase in [CO_2]), diminishing as CO_2 increased to 600 μmol mol^{-1} (0.4 g of pollen per 10 μmol mol^{-1} increase in [CO_2]). Floral spike number did not change from pre-industrial to current [CO_2], but pollen production per spikelet increased significantly (Fig. 1). From 370 to 600 μmol mol^{-1} CO_2, no further change in pollen production per spikelet was noted, but the number of floral spikes approximately doubled (Fig. 1). Analysis of the diameter of 200 individual pollen grains for each [CO_2] using a SEM (15 kV, ×1.5k) indicated no change in average pollen size (data not shown).

Small (non-significant) changes in total biomass (i.e. roots, stems and leaves) were observed by 21 DAS, and significant differences were observed by 29 DAS (Fig. 2). Significant differences in relative growth rate (RGR) also occurred by 29 DAS among [CO_2] treatments (0.174, 0.209 and 0.220 g g^{-1} day^{-1} for the 280, 370 and 600 μmol mol^{-1} [CO_2] treatments, respectively).

At seed maturity, total plant biomass was directly proportional to [CO_2]. From pre-industrial to current atmospheric [CO_2], leaf weight and stem weight increased by 36 and 49%, respectively, with no significant change in root or floral weight (Table 1). Leaf area, however, almost doubled in size for this same increase in [CO_2] (Table 1). At 600 μmol mol^{-1}, significant increases in all growth parameters at maturity were observed relative to the 370 and 280 μmol mol^{-1} treatments. The largest relative increase was observed for root weight which increased ~ 4-fold from 280 to 600 μmol mol^{-1} [CO_2]. No significant changes in stem to root ratio or specific leaf area occurred among [CO_2] treatments (data not shown).

Leaf photosynthesis, measured at the growth [CO_2], increased significantly with [CO_2], rising 170 and 250% from pre-industrial to current and future [CO_2], respectively, and 30% from current to future [CO_2] (Table 2). Values of assimilation at a measurement [CO_2] of 280 μmol mol^{-1} did not differ among [CO_2] treatments. However, at higher measurement CO_2 levels, leaves grown at 280 μmol mol^{-1} [CO_2] had significantly lower photosynthetic rates — an indication of down-regulation (Table 2). Acclimation was not observed between the 370 and 600 μmol mol^{-1} [CO_2] treatments. Analysis of the response of assimilation to internal CO_2 indicated no significant change in the initial slope of the response curve as a function of [CO_2] treatment. However, the internal CO_2 concentration where leaf assimilation is equal to zero (Γ^*, the CO_2 compensation point), and the maximum observed assimilation rate was lower for the 280 than the 370 and 600 μmol mol^{-1} treatments (data not shown).

Discussion

For many years, both botanists and health workers have been interested in those climatic and/or meteorological factors that influence atmospheric pollen concentration (e.g. Gregory 1973; Buck and Levetin 1982). Abiotic factors that influence pollen productivity such as rainfall, temperature and light also determine pollen amounts and severity of

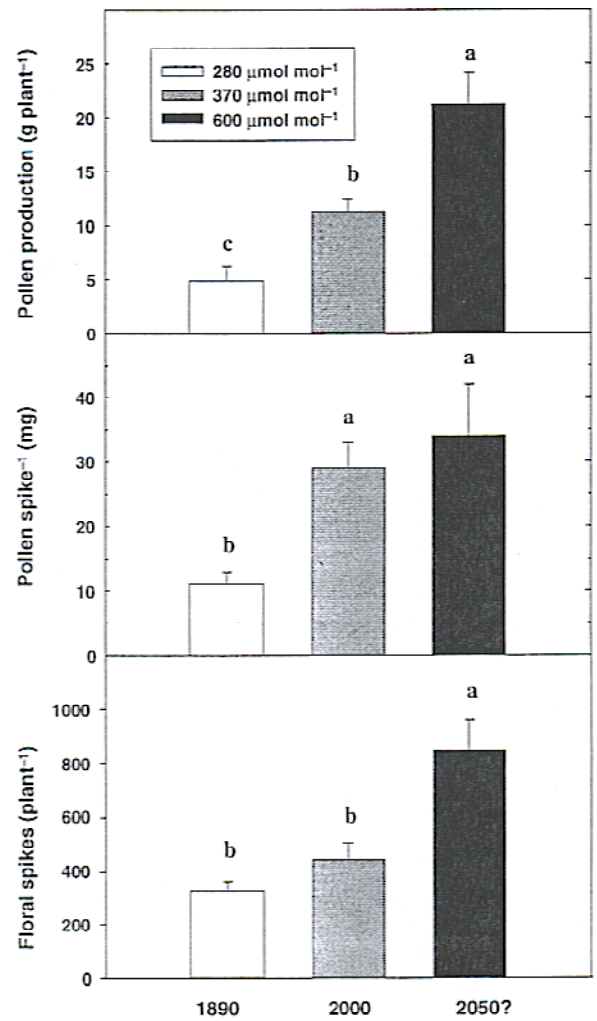

Fig. 1. Pollen production, pollen per floral spike and number of floral spikes in common ragweed grown at pre-industrial CO_2 concentrations (280 μmol mol^{-1}), current concentrations (370 μmol mol^{-1}) and a projected 21st century concentration (600 μmol mol^{-1}). Bars are ± s.e. Student–Newman–Keuls was used to determine differences among the [CO_2] treatments at the 0.05 significance level (a, b or c).

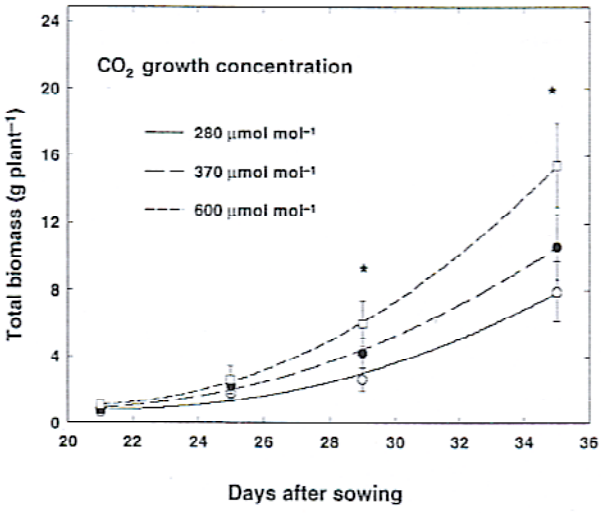

Fig. 2. Change in total plant biomass (g plant^{-1}) as a function of days after sowing (DAS) for ragweed grown at pre-industrial, current and future atmospheric [CO_2]. Bars are ± s.e. Relative growth rate (RGR) was determined between 21 and 29 DAS. No further change in RGR as a function of [CO_2] was observed after 35 DAS. * indicates a significant increase in total biomass relative to the 280 μmol mol^{-1} [CO_2] control.

allergies among susceptible populations during a given allergy season. Consequently, there has been a great deal of interest in modeling changes in pollen type and abundance associated with global climate change (Emberlin 1994). However, less is known concerning the direct stimulation of growth and pollen production of allergy-inducing species by rising [CO_2], one of the principal 'greenhouse' gases.

The observed stimulation in growth and photosynthesis observed here for ragweed is consistent with results seen elsewhere for C_3 species grown with enhanced [CO_2] (Kimball *et al.* 1993). Increasing the [CO_2] to 600 μmol mol^{-1} increased ragweed RGR within 4 weeks following emergence, and stimulated biomass at maturity almost 3-fold above pre-industrial [CO_2] values. Final vegetative biomass values obtained in the current experiment at ambient [CO_2] are consistent with those observed for single ragweed plants in abandoned agricultural fields at maturity (D. Patterson, pers. comm.). In the current study, both leaf area and weight were particularly sensitive to [CO_2]. The continued stimulation of single-leaf photosynthesis (at least through anthesis) and the observed increase in leaf area have obvious implications for maintaining a continued stimulation of photosynthesis and growth at the whole plant level with future CO_2 levels.

If growth of ragweed is indeed stimulated by increasing [CO_2], how does this alter subsequent reproductive effort? Floral spikes of ragweed contain both staminate and pistillate flowers. Pollen is wind-directed from numerous staminate flowers to pistillate heads, which are fewer in number and occur at the base of the floral spike (Bianchi *et al.* 1959). Because wind is the primary means of transport, large amounts of pollen are necessary to achieve seed set. Increasing vegetative growth provides both a structural platform for floral production and the carbon assimilate needed to produce flowers. In the current experiment, floral weight increased 70%, but floral weight as a percentage of total plant weight decreased (from 21% to 13%) from 280 to 600 μmol mol^{-1} CO_2. However, investment in pollen increased (from 3.6 to 6%) from 280 to 600 μmol mol^{-1} CO_2.

Because of the role of ragweed pollen in inducing allergies, the reproductive response of ragweed to rising atmospheric [CO_2] is of obvious interest. In the current study, the response of ragweed pollen production to rising [CO_2] was 2-fold. Increasing [CO_2] from pre-industrial to current levels increased the amount of pollen produced by an individual floral spike. As [CO_2] increased further to 600 μmol mol^{-1}, no additional increase in pollen per floral spike was observed, but the number of floral spikes rose significantly. The net result was an approximate doubling of pollen production capacity from pre-industrial to present day [CO_2] and a further doubling to a projected [CO_2] of 600 μmol mol^{-1}.

Interestingly, interpolation of the potential pollen response of ragweed to [CO_2] from the 1950s (~315 μmol mol^{-1}) to current levels shows a percentage

Table 1. Changes in measured (leaf area, leaf, stem and root dry weights) vegetative parameters at maturity for common ragweed (*Ambrosia artemisiifolia* L.) grown at pre-industrial, current and future levels of atmospheric [CO_2]

Different letters within a column indicate statistical differences between [CO_2] treatments at the 0.05 level according to Student–Newman–Keuls. Data are given on a per-plant basis

[CO_2] (μmol mol^{-1})	Area (m^2)	Weight (g)				Total weight (g)
		Leaf	Stem	Root	Floral	
280	1.15 c	65.1 c	30.7 c	11.3 b	28.9 b	135.1 c
370	2.17 b	88.7 b	45.7 b	13.5 b	35.7 b	183.6 b
600	3.41 a	178.9 a	97.1 a	50.3 a	49.2 a	372.4 a

Table 2. Photosynthesis (as CO_2 assimilation rate, μmol CO_2 m^{-2} s^{-1}) for ragweed (*Ambrosia artemisiifolia* L.) grown and measured at pre-industrial, current and future atmospheric [CO_2]

Different letters within a column indicate statistical differences between [CO_2] treatments at the 0.05 level according to Student–Newman–Keuls. Additional details are given in 'Materials and methods'

Growth [CO_2] (μmol mol^{-1})	Measurement [CO_2] (μmol mol^{-1})		
	280	370	600
280	15.1	23.3 b	33.1 b
370	19.6	40.7 a	53.0 a
600	14.8	35.6 a	52.9 a

increase in ragweed pollen consistent with the recent reported percentage increase in allergies and allergy-induced asthma among the general population (Platt-Mills and Carter 1997; Woolcock and Peat 1997). However, has the actual amount of ragweed pollen in the environment increased within the last 40 years? Because the rise in atmospheric [CO_2] has been so rapid, traditional ^{14}C dating techniques to determine *in situ* increases in pollen production since the mid-1950s are not applicable. The earliest pollen studies are based on some 13 000 gravity slide samples from 22 American cities summarized from 1916 to 1928 (Durham 1929). Unfortunately, direct comparisons between gravimetric and volumetric devices (e.g. Rotorod sampler) are difficult to perform. Differences in pollen recovery cannot be quantified, even roughly (see Frenz 1999*a*). Even if different sampling techniques were comparable, changes in land use and nitrogen deposition in industrial areas could not be separated from any direct atmospheric CO_2 effect. Current regional, on-site estimates of ragweed pollen production do not date back more than a few years (Frenz *et al.* 1995, Frenz 1999*b*), although it is hoped that these data could be used to verify potential increases in ragweed pollen with future increases in atmospheric [CO_2].

Will similar increases in pollen with enhanced [CO_2] be observed for other known allergy-inducing species? Projected increases in [CO_2] have been shown to stimulate the photosynthesis and growth of C_3 species such as lambsquarters (Carlson and Bazzaz 1982) and oak (Bunce 1992), as well as some C_4 species such as pigweed (Tremmel and Patterson 1993) and foxtail (Ziska and Bunce 1997). However, the reproductive response to [CO_2] cannot always be elucidated from observed increases in vegetative biomass (Jablonski 1997).

Critics of the role of CO_2 in climate change correctly point out that rising [CO_2] could result in a lush plant environment (Idso and Idso 1994). However, it should also be emphasized that the rise in [CO_2] is indiscriminatory with respect to the stimulation of both useful and noxious plant species. Furthermore, elimination of noxious weedy species by chemical means cannot always be assumed as atmospheric [CO_2] increases (Ziska *et al.* 1999). Consequently, the role of rising atmospheric [CO_2] with respect to distribution, growth and pollen production of weeds impacting human health should be of growing concern.

Acknowledgments

The authors thank Dr JA Bunce of the Climate Stress Laboratory for his suggestions to the manuscript, Dr Dave Patterson, weed specialist at North Carolina State University for his advice and Dr Linda Ford of the National Allergy Bureau for her insightful comments.

References

Ackerly DD, Bazzaz FA (1995) Plant growth and reproduction along CO_2 gradients: non-linear responses and implications for community change. *Global Change Biology* **1**, 199–207.

Bianchi DE, Schwemmin DJ, Wagner WH Jr (1959) Pollen release in the common ragweed (*Ambrosia artemisiifolia*). *Botanical Gazette* **120**, 235–243.

Buck P, Levetin E (1982). Weather patterns and ragweed pollen production in Tulsa, Oklahoma. *Annals of Allergy* **49**, 272–275.

Bunce JA (1992) Stomatal conductance, photosynthesis and respiration of temperate deciduous tree seedlings grown outdoors at an elevated concentration of carbon dioxide. *Plant, Cell and Environment* **15**, 541–549.

Carlson RW, Bazzaz FA (1982) Photosynthetic and growth response to fumigation with SO_2 at elevated CO_2 for C_3 and C_4 plants. *Oecologia* **54**, 50–54.

Curtis PS, Wang X (1998) A meta-analysis of elevated CO_2 effects on woody plant mass, form and physiology. *Oecologia* **113**, 299–313.

Deng X, Woodward FI (1998) The growth and yield responses of *Fragaria ananassa* to elevated CO_2 and N supply. *Annals of Botany* **81**, 67–71.

Durham OC (1929) Cooperative studies in ragweed pollen incidence: atmospheric data from twenty-two cities. *Journal of Allergy* **1**, 12–21.

Emberlin J (1994) The effects of patterns in climate and pollen abundance on allergy. *Allergy* **49**, 15–20.

Frenz DA (1999*a*) Comparing pollen and spore counts collected with the Rotorod sampler and Burkard spore trap. *Annals of Allergy Asthma & Immunology* **83**, 341–349.

Frenz DA (1999*b*) Volumetric ragweed pollen data for eight cities in the continental United States. *Annals Allergy Asthma and Immunology* **82**, 41–46.

Frenz DA, Palmer MA, Hokanson JM, Scamehorn RT (1995) Seasonal characteristics of ragweed pollen dispersal in the United States. *Annals of Allergy, Asthma and Immunology* **75**, 417–422.

Garbutt K, Bazzaz FA (1984) The effects of elevated CO_2 on plants: III. Flower, fruit and seed production and abortion. *New Phytologist* **98**, 443–446.

Gergen PJ, Turkeltaub PC (1992) The association of individual allergen reactivity with respiratory disease in a national sample: data from the second National Health and Nutrition Survey (NHANES II) *Journal of Allergy and Clinical Immunology* **90**, 579–588.

Gregory PH (1973) 'The microbiology of the atmosphere.' 2nd edn, 453 p. (John Wiley and Sons: Chichester, UK)

Houghton JT, Meira-Filho LG, Callander BA, Harris N, Kattenburg A, Maskell K (1996) 'IPCC climate change assessment 1995. The science of climate change.' (Cambridge University Press: Cambridge, UK)

Idso KE, Idso SB (1994) Plant responses to atmospheric CO_2 enrichment in the face of environmental constraints: a review of the past 10 years' research. *Agricultural and Forest Meteorology* **69**, 153–203.

Jablonski LM (1997) Response of vegetative and reproductive traits to elevated CO_2 and nitrogen in *Raphanus* varieties. *Canadian Journal of Botany* **75**, 533–545.

Keeling CD, Whorf TP (1994) Atmospheric CO_2 records from sites in the SIO air sampling network. In 'Trends '93: a compendium of data on global change'. (Eds TA Boden, DP Kaiser, RJ Sepanski and FW Stoss) pp. 20–26. (Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory: Oak Ridge, TN)

Kimball BA, Mauney JR, Nakayama FS, Idso SB (1993) Effects of increasing atmospheric CO_2 on vegetation. *Vegetatio* **104/105**, 65–75.

Lawlor DW, Mitchell RAC (1991) The effects of increasing CO_2 on crop photosynthesis and productivity: a review of field studies. *Plant, Cell and Environment* **14**, 807–818.

Meggs WJ, Dunn KA, Bloch RM, Goodman PE, Davidoff AL (1996) Prevalence and nature of allergy and chemical sensitivity in a general population. *Archives of Environmental Health* **51**, 275–282.

Platts-Mills TAE, Carter MC (1997) Asthma and indoor exposure to allergens. *New England Journal of Medicine* **336**, 1382–1384.

Poorter H (1993) Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. *Vegetatio* **104/105**, 77–97.

Reekie JYC, Hicklenton J, Reekie EG (1997) The interactive effects of carbon dioxide enrichment and daylength on growth and development in *Petunia hybrida*. *Annals of Botany* **80**, 57–64.

Robinson JM (1984) Photosynthetic carbon metabolism in leaves and isolated chloroplasts from spinach plants grown under short and intermediate photosynthetic periods. *Plant Physiology* **75**, 397–409.

Tremmel DC, Patterson DT (1993) Responses of soybean and five weeds to CO_2 enrichment under two temperature regimes. *Canadian Journal of Plant Science* **73**, 1249–1260.

Woolcock AJ, Peat JK (1997) Evidence for the increase in asthma worldwide. In 'The rising trends in asthma, Ciba foundation symposium 206'. (Eds D Chadwick and G Cardew) pp. 123–125. (John Wiley and Sons: Chichester, UK)

Ziska LH, Bunce JA (1997) Influence of increasing carbon dioxide concentration on the photosynthetic and growth stimulation of selected C_4 crops and weeds. *Photosynthesis Research* **54**, 199–208.

Ziska LH, Teasdale JR, Bunce JA (1999) Future atmospheric carbon dioxide may increase tolerance to glyphosate. *Weed Science* **47**, 608–615.

Manuscript received 25 February 2000, accepted 3 July 2000