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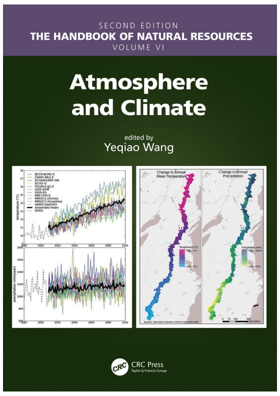

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Air Pollutants: Elevated Carbon Dioxide

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Air Pollutants: Elevated Carbon Dioxide

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Introduction

The concentrations of various compounds in the atmosphere have changed during the last century, and they continue to change. Most of these compounds interact with the terrestrial biosphere as they are part of the overall biogeochemical cycling of, e.g., carbon, oxygen, nitrogen, and sulfur.[1] For example, depending on their concentrations, gaseous compounds [sulfur dioxide (SO_2), nitrogen monoxide and dioxide (NO_2/NO)] may be beneficial to terrestrial ecosystems or remain inert (O_3) at low concentrations, whereas at higher levels, they may act as air pollutants affecting these systems in an adverse manner. Although atmospheric CO_2 is the basic plant resource for photosynthesis, its current concentration is still limiting C_3 plant growth. The rapid increase of the global atmospheric CO_2 concentration [CO_2], along with the overall changes in climate and atmospheric chemistry, require an assessment of the potential future interactive effects of air pollutants and elevated [CO_2] on terrestrial ecosystems.

Atmospheric Change: Concentrations and Trends

On a global scale, the concentrations of a variety of gaseous and particulate compounds in the atmosphere, including CO_2, NO/NO_2, SO_2, O_3, ammonia (NH_3), heavy metals, and volatile organic compounds (VOC) have undergone temporal and spatial changes during the last century.[2] After peak emissions in the 1960s to the 1980s in industrialized countries particularly, the concentrations of SO_2, and to a smaller extent of NO_x (NO/NO_2), VOCs, and particulate matter, have declined during the past decades in Europe and North America. NH_3, which is the most important reduced N species, is of importance as a direct air pollutant in the vicinity of local emitters. However, wet and dry N deposition from oxidized and reduced N species are predicted to increase in other regions of the world.[3] The occurrence and distribution of airborne VOCs are difficult to assess because there are both anthropogenic and biogenic sources. With respect to heavy metals such as lead (Pb), cadmium (Cd), nickel (Ni), mercury (Hg), and zinc (Zn), a decline in emission and subsequent deposition was observed in most of Europe since the late 1980s. Unlike the development in Europe and North America, emissions and consequently atmospheric concentrations of many of the above-mentioned compounds have been increasing over the last two decades particularly in the rapidly growing regions of Asia, Africa, and Latin America.[4] For example, China and India are now the leading emitters of SO_2 in the world. Also, the predicted further increase in global nitrogen oxide (NO_x) emissions may be attributed largely to these countries. On the other hand, concentrations of ground-level O_3 and atmospheric CO_2 have increased and continue to increase on a global scale. In most industrialized countries, O_3 concentration [O_3] has nearly doubled during the last 100 years. Current background [O_3] in the Northern hemisphere is within the range of 23–34 ppbv (parts-per-billion by volume). Although at least in most parts of Western Europe there is a clear trend of decreasing O_3 peak values ("photosmog episodes"), models predict that background [O_3] will continue to increase at a rate of 0.5% to 2% per year in the Northern Hemisphere during the next several decades, and that global surface [O_3] is expected to be in the range of 42–84 ppbv by 2100.[5] O_3 pollution has also become a major environmental problem in many of the countries with rapidly developing population and related economic growth, respectively. O_3 is currently considered the most important atmospheric pollutant that has direct negative effects on vegetation worldwide. Its concentrations vary considerably in time and space and show distinct annual and diurnal patterns.

Since the beginning of the 19th century, the CO_2 in the atmosphere has increased globally from approximately 280 ppmv (parts-per-million by volume) to current values of about 395 ppmv. It is expected that CO_2 will continue to increase even more rapidly and may reach about 550–650 ppmv between 2050 and 2070.[6] CO_2 is the substrate for plant photosynthesis, and its current atmospheric concentration is limiting for photosynthesis and growth of C_3 plants. It is expected that the increase in CO_2 will have far-reaching consequences for most types of vegetation.

Effects of O_3 and CO_2 Alone

Due to their global importance and their contrasting effects on vegetation, plant growth responses to either O_3 or CO_2 alone are briefly described. Primary O_3 effects include subtle biochemical and ultrastructural changes in the plant cell, which may result in impaired photosynthesis, alterations of carbon allocation patterns, symptoms of visible injury, enhanced senescence, reduced growth and economic yield, altered resistance to other abiotic and biotic stresses, or reduced flowering and seed production at the whole-plant level[7,8] At the ecosystem level, this may result in a loss of competitive abilities of plant species in communities along with shifts in biodiversity and impaired ecosystem functions and services like reduced carbon sequestration and altered hydrology.[9] For example, current ambient (O_3) in many industrialized areas has been shown to suppress crop yields of sensitive species and to retard growth and development of trees and other plant species of the non-woody (semi)natural vegetation. Overall quantification of O_3 effects on vegetation is complicated by large inter- and intra-specific variability in the O_3 susceptibility of plants.[10]

By contrast, plants of the C_3 type most frequently respond to elevated CO_2 with a stimulation of photosynthesis accompanied by a reduced stomatal conductance and transpiration rate, an enhanced concentrations of soluble carbohydrates, and a stimulation of biomass production and economic yield.[11] Similarly, in C_4 plants, higher CO_2 concentrations reduce stomatal conductance and transpiration, i.e., both C_3 and C_4 plants may benefit from elevated CO_2 by improved water-use efficiency and a reduced demand for water. Under well-watered conditions, no significant growth stimulation has been found so far in C_4 plants, because C_4 photosynthesis is saturated under ambient CO_2.[12,13] Growth and yield enhancements of up to 25–35% as compared to ambient CO_2 have been observed when crop plants were exposed to 550–750 ppmv CO_2. Experiments with tree species ranging from short-term studies with seedlings to long-term whole-stand manipulations have also shown that elevated CO_2 stimulated net photosynthesis and resulted in enhanced tree growth in almost all cases.[14,15] As with O_3, plant species

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differ widely in their response to high CO_2, which makes an overall assessment of its potential effects on vegetation difficult.

Interactive Effects of Air Pollutants and CO_2

Along with the ongoing and predicted further changes of global climate and atmospheric chemistry, there is considerable interest in how terrestrial ecosystems will respond to these multiple environmental changes and particularly how the individual changes in atmospheric constituents may interact with each other when they impact vegetation. The majority of studies dealing with this issue have addressed two-way interactions of O_3 and elevated CO_2, although there is much less information on how other air pollutants interact with high CO_2. There are no studies describing three-way interactions, i.e., in which two air pollution components and elevated CO_2 are combined together. In a biological sense, the combined action of multiple factors in comparison to single-factor effects can be described as additive (effect directly predictable from single-factor treatment) or as interactive. Interactive effects can be synergistic (effect > than expected from single-factor treatment) or antagonistic (effect < than expected from single-factor treatment).[16]

CO_2 and O_3

A great number of previous and more recent studies using different experimental approaches ranging from controlled environment to free-air O_3- and CO_2-enrichment systems have been carried out on the combined effects of the two gases. The bulk of these studies has shown that high CO_2 in the range of 200–400 ppmv above current ambient CO_2 levels either partially or totally compensates for adverse O_3 effects, whether these effects have been addressed at the biochemical and physiological level or at the whole-plant level including growth and yield. This has been demonstrated for crop (e.g., wheat, soybean, potato, rice) as well as for tree (e.g., trembling aspen, paper birch, sugar maple) species, although little information is available for grassland species.[17–20] For example, elevated CO_2 reduces O_3 effects, such as a loss in root and main stem biomass, a decrease in leaf area and mass, general foliar damage, lower growth and yield, lower starch levels, and an altered carbon balance. Results from recent free-air concentration enrichment (FACE) studies, however, have indicated that the mitigating effect of elevated CO_2 against O_3 damage might be less than predicted from earlier chamber studies.[12]

The proposed mechanisms to explain the protective effect of elevated CO_2 against the phytotoxic effects of O_3 include the following: i) reduced uptake or flux of O_3 through the stomata due to a CO_2-induced stomatal closure, ii) improved supply of carbon skeletons supporting the synthesis of antioxidants involved in the scavenging of O_3 and its toxic products, iii) protection of the RuBisCo protein from O_3-induced degradation, and iv) CO_2-induced changes in the cell surface/volume ratio.[9,21,22] However, it has been shown that in spite of decreased stomatal conductance under elevated CO_2, adverse effects of O_3 may still occur.[8,19] Additionally, elevated O_3 has been found to impair stomatal responsiveness to CO_2, i.e., O_3 causes less-sensitive ("sluggish") stomatal responses to elevated CO_2.[23] As CO_2 effects on stomatal conductance may be species specific, it is not yet possible to support a general concept of a CO_2-induced reduction in the flux of O_3 into the plant. Nevertheless, a reduction in stomatal conductance and thus in the O_3 uptake may increase atmospheric O_3 in the boundary layer.[24] Moreover, in a given plant species, protection by high CO_2 from a particular adverse effect is not necessarily associated with the protection against another adverse effect. For instance, in wheat plants, elevated CO_2 provided full protection from effects of O_3 on total plant biomass, but not on grain yield. From the available database of studies that have examined the interactive effects of O_3 and CO_2, the information is not entirely consistent, as several studies revealed that elevated CO_2 may not always protect plants from the adverse effects of O_3 (Table 3.1).

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TABLE 3.1 Selected Examples of the Effects of Elevated O_3 and CO_2, Alone or in Combination, on Plant Responses (Examples with Significant Adverse Effects of O_3 on Visible Injury, Photosynthesis, Growth, and Yield)

Species	O_3 Effect	CO_2 Effect	O_3/CO_2 Effect
Potato	Decreased chlorophyll content; visible foliar leaf injury	n. e.	Adverse effect of O_3 on chlorophyll content unchanged; reduced degree of visible O_3-induced leaf injury
Wheat	Visible leaf injury; reduced photosynthesis; reduced growth; reduced yield	Increased photosynthesis; increased growth; increased yield	Reduced degree of visible O_3-induced leaf injury; amelioration of negative O_3 effects on photosynthesis, growth, and yield
Soybean	Reduced photosynthesis; reduced growth; reduced seed yield	Increased photosynthesis; increased growth; insignificant increase of seed yield	O_3 impact on photosynthesis lessened; amelioration of negative O_3 effects on photosynthesis, growth, and yield
Cotton	Reduced leaf area per mass; reduced starch contents	Increased leaf area per mass and starch contents	Prevention of adverse effects of O_3 by CO_2
Norway spruce	Visible leaf injury (chlorotic mottling)	n.e.	No effect of CO_2 on the degree of O_3-induced leaf injury
Trembling aspen (different O_3-sensitive and -tolerant clones)	Reduced tree growth parameters (height, diameter, volume)	Enhancement of growth parameters	No effect of CO_2 on the degree of O_3-induced growth reductions
Paper birch	Reduced photosynthesis; decreased dry matter production	Increased photosynthesis; increased dry matter production	Decrease in photosynthesis and dry matter production similar to O_3 alone
White clover (sensitive clone)	Visible leaf injury	n.e.	Little effect on the degree of O_3-induced foliar injury

Source: Adapted from Karnosky et al.,[19] Vandermeiren et al.,[20] Polle & Pell,[21] and Runeckles.[26] Abbreviations: CO_2, carbon dioxide; n.e., No effect; O_3, Ozone.

CO_2 and Other Air Pollutants

Very few studies have addressed the combined effects of elevated CO_2 and of other air pollutants. SO_2 has long been known to adversely affect agricultural crops and forest plants above a certain threshold concentration.[25] Reduced photosynthesis, altered water relations, growth retardations, yield losses, and altered susceptibilities to other stresses are common plant responses observed under SO_2 stress. Due to the diminishing importance of SO_2 as a widespread air pollutant, few studies have been conducted on the combined action of SO_2 and elevated CO_2. In earlier studies, it was shown for some crop species that elevated CO_2 reduced the sensitivity of the plants to SO_2 injury or protected them from the negative effects of SO_2 on growth and yield.[26] With the combined exposure of crop species to both gases, the yield increments were sometimes even larger when compared to the stimulation observed with exposure to elevated CO_2 alone, suggesting that the plants were able to use the airborne sulfur more effectively under the conditions of enhanced carbon availability. Low-to-moderate SO_2 concentrations may confer a nutritional benefit to plants, particularly under conditions of low sulfur availability in the soil.

Studies on the interactive effects of elevated CO_2 and nitrogen oxides (NO and NO_2) are confined to commercial greenhouses under conditions of horticultural crop production under very high CO_2 and are not considered here. However, it has been shown repeatedly that positive plant growth responses to elevated CO_2 are smaller at low relative to high soil N supply. This is related to the question on the role of future atmospheric N deposition and "aerial carbon fertilization" by elevated CO_2 in shaping the size of the terrestrial carbon sink and how plant biodiversity might be affected by these inputs. Assuming that aerial N supply via enhanced N deposition causes similar effects as soil N fertilization, a few experimental and modeling studies addressed the question of how elevated CO_2 interacts with N deposition. For example, it has been shown that N addition enhanced the CO_2 stimulation of plant productivity in the first phase of a multiyear CO_2–N manipulation study with a herbaceous wetland plant community. But in the longer term, the observed N-induced shift in the plant community composition suppressed the CO_2 stimulation of plant productivity, indicating that plant community shifts can act as a feedback effect that alters ecosystem responses to elevated CO_2.[27] In a long-term study with simulated grassland systems with 16 species, high N supply reduced species richness by 16% under ambient CO_2 but only by 8% under elevated CO_2, i.e., high CO_2 ameliorated negative N effects.[28,29] Elevated CO_2 and N addition have been found to affect above and belowground C allocation in temperate forest trees in an opposite way, i.e., elevated CO_2 increases belowground allocation, whereas N increases aboveground allocation; however, the ratio of above vs. belowground C flow does not change in the combination of both treatments.[30]

Conclusion

The assessment of the potential combined effects of air pollutants and elevated atmospheric concentrations of CO_2 on vegetation is of critical importance during the next decades. Interactive effects of these atmospheric compounds on crops, trees, and other types of vegetation have been shown. Existing evidence on such interactions is almost entirely restricted to CO_2 and O_3, the concentrations of which are increasing globally. Although rising CO_2 will be mostly beneficial to plants, current ambient O_3 are high enough to impair plants in many regions of the world. There is prevailing information that elevated CO_2 may protect plants from adverse effects of O_3, but this has not been demonstrated unequivocally. There is also some information that rising CO_2 may protect plants against phytotoxic SO_2 concentrations. The future interactions of elevated CO_2 and enhanced atmospheric N deposition are of concern in many ecosystem types with respect to carbon sequestration and biodiversity. Overall, our understanding has to be improved about how other growth variables, such as plant genotype, soil water deficit, nutrient availability, or temperature, may modify the interaction between air pollutants and elevated CO_2.

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