The Effects of Tropospheric Ozone on Net Primary Productivity and Implications for Climate Change*

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Keywords

Abstract

Tropospheric ozone (O_3) is a global air pollutant that causes billions of dollars in lost plant productivity annually. It is an important anthropogenic greenhouse gas, and as a secondary air pollutant, it is present at high concentrations in rural areas far from industrial sources. It also reduces plant productivity by entering leaves through the stomata, generating other reactive oxygen species and causing oxidative stress, which in turn decreases photosynthesis, plant growth, and biomass accumulation. The deposition of O_3 into vegetation through stomata is an important sink for tropospheric O_3, but this sink is modified by other aspects of environmental change, including rising atmospheric carbon dioxide concentrations, rising temperature, altered precipitation, and nitrogen availability. We review the atmospheric chemistry governing tropospheric O_3 mass balance, the effects of O_3 on stomatal conductance and net primary productivity, and implications for agriculture, carbon sequestration, and climate change.

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INTRODUCTION

Tropospheric ozone (O_3) is a damaging air pollutant that significantly impacts human and ecosystem health, and is also an important greenhouse gas responsible for direct radiative forcing of 0.35–0.37 W m^{-2} on the climate (52, 136). It is estimated to have been responsible for 5%–16% of the global temperature change since preindustrial times (52) and is the second-most-important air pollutant (after particulate matter) in causing human mortality and morbidity impacts to human health; globally, an estimated 0.7 million deaths per year are attributed to anthropogenic O_3 pollution

(8; see sidebar Ozone Effects on Human Health). The damaging effects of O_3 on photosynthetic carbon assimilation, stomatal conductance, and plant growth feed forward to reduce crop yields (3, 10, 46, 49, 57), with current global economic losses estimated to cost from \$14 billion to \$26 billion (151). Forests and natural ecosystems are also negatively impacted by current O_3 concentrations ([O_3]) (66, 162), which have downstream consequences for ecosystem goods and services (126).

Experimental and modeling approaches are currently being used to understand plant responses to elevated [O_3] and to predict their impacts on global net primary productivity (NPP); however, significant gaps in knowledge remain about the interactions of rising tropospheric [O_3] and other environmental factors, including drought, soil nutrient status, and variables associated with climate change [e.g., elevated carbon dioxide concentration ([CO_2]) and rising temperature]. In addition to being a direct driver of global warming, tropospheric [O_3] can also induce indirect effects. For example, increasing atmospheric [O_3] will negatively impact plant production, reducing the ability of ecosystems to sequester carbon, and thus indirectly feed back on atmospheric [CO_2], enhancing climate change (31, 138).

In this review, we outline the processes that govern tropospheric O_3 mass balance in the atmosphere and the effects of O_3 on NPP, crop yield, and other ecosystem services. We also discuss the interaction of plant responses to O_3 and other stresses caused by environmental change, with particular consideration of the implications for future climate change.

TROPOSPHERIC OZONE CONCENTRATIONS

Globally, the majority of tropospheric O_3 comes from photochemical reactions of methane (CH_4), volatile organic compounds (VOCs), and NO_x, which are largely from anthropogenic emissions. A minor component (approximately 10%) of tropospheric O_3 comes from stratospheric influx (139). Background

[O_3] has risen from less than ~10 ppb before the industrial revolution (155) to daytime summer concentrations exceeding 40 ppb in many parts of the Northern Hemisphere (53, 139). Future [O_3] will depend upon O_3 precursor emissions, which are expected to change significantly with population growth, economic development, technological progress and its adoption, policy changes, land use changes, and climate and other environmental changes over this century (126).

Ozone Chemistry in the Troposphere

A full description of the complex set of reactions involved in formation and destruction of O_3 in the troposphere is beyond the scope of this review (for more coverage of this topic, see 48, 126); however, here we provide an introduction to the processes controlling O_3 formation and destruction and how they vary in different regions of the globe. The chemistry of O_3 formation requires photolysis and is more rapid at higher temperatures. Therefore, high O_3 production occurs in conditions of strong sunlight and high temperatures, which can also favor maximum plant photosynthesis and growth in temperate ecosystems. However, extremes of sunlight and temperature can lead to plant stress, in which case high [O_3] and maximum stomatal conductance and O_3 uptake are no longer coincident.

The sensitivity of O_3 production to emissions depends on the levels of NO_x. In rural areas of industrialized countries with moderate NO_x levels, O_3 formation reactions dominate. In these regions, which include many of the major crop-growing areas of the world, the rate of O_3 formation increases with increasing [NO_x], and O_3 formation is referred to as NO_x limited. In contrast, O_3 formation is inhibited by increasing [NO_x] in urban locations with very high levels of NO_x (~1,000 parts per trillion), and O_3 in these regions is referred to as VOC limited (126). In these urban areas, legislation-enforced reduction of NO_x emissions will increase [O_3], exposing urban populations to higher O_3 doses (126). Only by more stringent controls of both NO_x and VOCs will O_3 be effectively controlled in both urban city cores and downwind suburban and rural areas (48).

OZONE EFFECTS ON HUMAN HEALTH

On the basis of cardiopulmonary and lung cancer mortality rates and through use of a global atmospheric chemical transport model, anthropogenic [O_3] was estimated to result in approximately 0.7 million ± 0.3 million respiratory mortalities annually worldwide, corresponding to 6.3 million ± 3.0 million years of lost life (8). More than 75% of O_3-induced mortalities were estimated to occur in the densely populated and heavily polluted Asian continent. O_3-induced mortalities were greatest in highly populated areas, but also occurred in rural areas affected by the increased regional or global background of air pollution since preindustrial times.

Deposition of Ozone

The main removal process for O_3 in the boundary layer (the few hundred meters nearest the earth's surface) is deposition to the surface, known as dry deposition. The rates of dry deposition to land surfaces are typically an order of magnitude greater than the rates of deposition to marine surfaces. Dry deposition to terrestrial ecosystems is controlled largely by stomata, which are responsible for 30%–90% of total ecosystem O_3 uptake (29, 54). There is therefore a correlation between stomatal conductance and potential O_3 damage, as noted by Reich & Amundson (128) when they reported that crops and trees with higher rates of stomatal conductance were more negatively impacted by O_3 than trees with lower rates of stomatal conductance. Greater O_3 sensitivity in angiosperms compared with gymnosperms (127, 161) and screens of different genotypes within species have confirmed the association between higher rates of stomatal conductance and O_3 sensitivity (22, 24, 89).

Stomata do not exclusively control ecosystem O_3 uptake. In environments where high light and temperature cause midday depression in photosynthesis, times of maximum stomatal

conductance do not coincide with peak $[O_3]$, which can reduce potential oxidative damage (43). In some ecosystems, nighttime flux can account for as much as 10%–25% of the diel flux (63, 100). The highest O_3 pollution episodes also occur during heat waves, which again are periods of low stomatal conductance. (Further dependence on environmental factors is discussed in Interactions, Feedbacks, and Climate Change, below.) Because the plant damage depends on the flux of O_3 into plant tissues rather than on the external atmospheric concentration, metrics for O_3 damage based on the stomatal flux into the plant and not just atmospheric $[O_3]$ are more suitable for O_3-risk assessment (43).

Nonstomatal sinks for O_3 removal can also be important in determining O_3 loss from the atmosphere, especially outside of the growing season, when stomatal conductance is limited or (in the absence of leaf biomass) nonexistent (100). Nonstomatal O_3 deposition to plant cuticles and other surfaces as well as soil is dependent on factors such as leaf and soil wetness, soil texture, and canopy structure (100). In addition, reactions such as thermal decomposition on the leaf surface, O_3 reactions with biogenic VOCs (such as isoprene) and soil NO_x emissions are important for destruction of O_3 at the stand and ecosystem scale (71, 147). These nonstomatal O_3 removal processes are not harmful to the plants, and by destroying O_3 they reduce its overall damaging effect (61).

Current and Future Ozone Trends

Current $[O_3]$ is considerably higher in the Northern Hemisphere than the Southern Hemisphere, with background monthly mean $[O_3]$ in the Northern Hemisphere ranging from 35 to 50 ppb (41, 139). In North America and Europe, higher $[O_3]$ occurs in the summer, with peak daily concentrations occurring in the late afternoon. Very high concentrations episodically occur, with O_3 levels reaching 200–400 ppb in metropolitan areas or in more remote areas during heat waves (126). Global assessments of $[O_3]$ trends rely on modeled

estimates from chemistry transport models that are driven by meteorological data sets and anthropogenic emissions inventories (e.g., 41, 139). These models predict O_3 at different altitudes in the troposphere and generally show good agreement at the ground level (139). **Supplemental Video 1** (follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**) animates global $[O_3]$ estimates from June 2010 to July 2011 based on outputs from the MOZART-4 model (41), showing the notable trend of higher $[O_3]$ in the Northern Hemisphere compared with the Southern Hemisphere, with North America, the Mediterranean, and South and Southeast Asia having seasonally high $[O_3]$.

Global photochemical modeling studies performed for the Hemispheric Transport of Air Pollution 2010 assessment (33) provided estimates of recent trends in surface $[O_3]$ for the regions that currently show the highest $[O_3]$. These models indicate recent reductions in peak surface $[O_3]$ for North America and Europe, which are likely to have been due to effective controls on NO_x and VOCs over the past two decades in response to the Clean Air Act in the United States and the Long-Range Transboundary Air Pollution Convention and European Union targets in Europe. In contrast, O_3 levels in Asia are continuing on an upward trend owing to continued rapid industrialization across the region. However, it should be noted that these regional trends hide large local variations in the direction of changes in surface concentrations; for example, many parts of the western United States are actually seeing increases in springtime surface $[O_3]$ (33).

Estimates of future surface $[O_3]$ depend on emissions and legislation scenarios and can vary from decreases from 2000 to 2030 of around 2 ppb globally in the cleanest case to increases of around 4 ppb in the most polluted case (34). These have differing consequences for plant damage, which are explored in Interactions, Feedbacks, and Climate Change (below). Increased temperatures and associated water vapor result in decreased surface O_3 in cleaner

regions but tend to have the opposite effect in more polluted areas. A larger predicted influx of stratospheric O_3 under climate-change conditions would lead to an increase in tropospheric $[O_3]$ (34).

Regulation of Ozone Concentrations

Currently, existing global and regional agreements established to control O_3 target only its role in degrading air quality, and even though it is a greenhouse gas, it is not dealt with in the Kyoto Protocol, the mechanism of implementation of the United Nations Framework Convention on Climate Change. The only globally defined limit (air quality guideline) for O_3 has been established by the World Health Organization as a guideline to protect human health. In North America, air quality guidelines are established only for the protection of human health, with discussions ongoing as to whether to establish guidelines designed to also protect ecosystems. Only in Europe have a number of organizations set numerical targets for O_3 to protect both human health and ecosystems (see **Supplemental Table 1**).

The air quality guidelines that have been established for ecosystems are based on the derivation of dose-response relationships (DRs) from comparable experimental data. DRs have been developed in North America and Europe based on data from the National Crop Loss Assessment Network (NCLAN) (69) and European Open Top Chamber (EOTC) (78) programs, respectively. These data described yield and growth responses for a range of crop species (and a far more limited number of forest and grassland species) that were used to define O_3 metrics and subsequently DRs. The development of these DRs has seen an evolution in the O_3 metrics used to characterize exposure from growing-season averages to metrics that accumulate O_3 exposure over the growing season, emphasizing higher concentrations (sometimes with a phenological weighting) to capture those concentrations considered most harmful to plants. Most recently, metrics have been developed that relate O_3 damage to accu-

mulated O_3 dose (i.e., the O_3 taken up via the stomata) rather than to ambient concentration (11). These flux-based metrics have the benefit of incorporating some of the species-specific (e.g., plant phenological and physiological characteristics) and environmental (stomatal conductance response to temperature and atmospheric and soil water status) factors that have been identified as determining plant response to O_3 stress (59). They also have the advantage of being able to capture changes in both diurnal and seasonal $[O_3]$ profiles. Most important, comparisons of DRs for a number of crop (119) and forest (81) species have found that the prediction of yield and biomass response to O_3 is improved when O_3 is characterized by flux-based rather than concentration-based metrics.

An important development in Europe has been the integration of such flux-based methods—originally designed to assess O_3 damage to ecosystems—within the dry deposition schemes of photochemical models such that estimates of O_3 loss from the atmosphere can also benefit from the improved understanding of the stomatal deposition processes. A number of dry deposition algorithms already included such stomatal control of deposition processes (122, 156), but only the Deposition of Ozone and Stomatal Exchange (DO_3SE) model (39), which is currently incorporated into the European Monitoring and Evaluation Programme photochemical model (137), is formulated such that consistency exists between estimates of dry deposition and estimates of O_3 damage to ecosystems. This tool has been instrumental in Europe in developing targeted, effects-based O_3 precursor emission control policy for the region (98). As our understanding of the mechanisms by which O_3 causes damage within plants improves (reviewed in the following section), methods could be developed to integrate the most important factors determining plant, and possibly ecosystem, response to an effective O_3 dose. This will allow more reliable extrapolation of risk assessment methods into global regions other than the one where they were originally developed and under altered climate regimes.

▶ Supplemental Material

OZONE EFFECTS ON CARBON UPTAKE, ASSIMILATION, AND UTILIZATION

The rate of O_3 penetration into the leaf and the capacity of the leaf to tolerate the reactive oxygen species (ROS) generated from O_3 are major control points of the downstream effects of O_3 on NPP; together, they constitute the effective flux of O_3 into leaves (38, 111). O_3 movement into the intercellular space of the mesophyll is controlled largely by stomatal aperture. Once inside, O_3 reacts rapidly in the apoplast with a number of potential molecules to produce other ROS, including hydrogen peroxide, superoxide radicals, hydroxyl (OH^-) radicals, and NO (2, 62, 68, 107), making the ROS quenching capacity of the apoplast the first line of defense against O_3 damage (32, 107). Following transient exposure to high levels of O_3 (often exceeding 150 ppb and termed acute in the literature), perception of stress involves ROS, hormones, Ca^{2+}, and mitogen-activated protein kinase (MAPK) signaling cascades.

There is significant overlap between the O_3 response pathway and programmed cell death induced by pathogens (for reviews, see 12, 32, 79, 113). Both stresses amplify ROS production, which activates ethylene, salicylic acid, and jasmonic acid signaling pathways to induce the expression of defense genes. The current evidence suggests that ethylene promotes endogenous ROS formation and lesion propagation, salicylic acid is required for programmed cell death, and jasmonic acid limits the spread of lesions from cell to cell (79, 113). However, chronic O_3 exposure that is commonly reported today in polluted regions does not always elicit visible cell death symptoms; instead, chronic O_3 decreases photosynthesis and plant biomass and causes early senescence (49, 116, 127). The mechanistic and transcriptional responses of plants to chronic O_3 treatments are often very different from the responses of plants to acute O_3 treatments in controlled environments (26, 28, 65, 93, 105), making it difficult to extrapolate results from short-term acute experiments to plants experiencing chronic concentrations in natural environments. In this section, we discuss recent studies of stomatal regulation of O_3 uptake and review the effects of chronic O_3 on mechanisms governing NPP, including reductions in carbon gain via decreased rates of CO_2 assimilation, increased ROS scavenging and detoxification, altered allocation of carbon to plant parts, and the carbon cost of increased protein turnover or repair and accelerated senescence.

Effects of Ozone on Stomatal Conductance

Exposure of *Arabidopsis* to acute O_3 results in a rapid transient decrease in stomatal conductance (within 3–6 min of exposure) accompanied by a burst of ROS in the guard cells, followed by a slower recovery to initial rates of stomatal conductance (89, 150). This transient decrease is not thought to be related to altered photosynthetic rate within the mesophyll or to damage to the guard cells, as full recovery is seen within 30–40 min (89). A minimum $[O_3]$ of 80 ppb is required to trigger the rapid transient decrease in stomatal conductance described above (150). However, long-term chronic O_3 exposure at lower concentrations typically also results in lower stomatal conductance, which is not transient or reversible (reviewed by 108, 128, 161). A change in stomatal conductance in plants exposed to chronic elevated O_3 has been attributed to a direct effect of O_3 on photosynthesis, which results in increased internal $[CO_2]$ and in turn lower stomatal conductance (128). However, this mechanism is not supported in all studies (115); in fact, studies also report that stomata are impaired by chronic O_3 exposure and are unable to close rapidly in response to environmental stimuli (13, 102). There is also more recent evidence that stomatal conductance is not universally decreased by chronic elevated $[O_3]$, but that leaf age and plant developmental stage can alter the degree to which O_3 affects stomatal conductance (18, 149). Additionally, stomatal sensitivity to abscisic acid may be compromised in O_3-stressed plants (106, 159, 160). The

implications of this finding are that when plants are exposed to both drought and O_3 stress, they will continue to lose water despite the potential for dehydration (159). However, these recent findings contrast with the long-held belief and considerable experimental evidence that drought ameliorates the impact of O_3 because drought causes stomatal closure and thereby reduces O_3 flux into leaves. More research is needed to test whether the loss of sensitivity to abscisic acid is specific to the species and conditions tested to date, or is a general feature of plant responses to O_3. Regardless, the interactions of O_3 with other environmental factors and with plant development are important determinants of the stomatal response.

Direct Effects of Ozone on Primary Metabolism

It is well established that plant growth in chronic O_3 is characterized by decreased rates of CO_2 assimilation at the leaf level (10, 49), which constitutes the basis for O_3-mediated reductions in ecosystem NPP (**Figure 1**). Several meta-analyses of crop and tree species have evaluated the impact of O_3 on light-saturated photosynthesis (A_{sat}) and revealed that although no change was observed for the gymnosperm tree species examined (161), A_{sat} in angiosperm trees, soybean (*Glycine max*), wheat (*Triticum aestivum*), and rice (*Oryza sativa*) was significantly decreased by ambient or near-ambient [O_3] (3, 46, 108, 161). Consistent with the changes in A_{sat}, nonstructural carbohydrates essential for growth, including sucrose and starch, also decreased. O_3-induced decreases in primary metabolism are well correlated with the capacity at the cellular level for CO_2 fixation, based on studies of RuBisCO transcript levels, protein level, and enzyme activity (**Supplemental Table 2**). Additional molecular studies examining global proteomic changes in wheat and rice have detected similar changes in RuBisCO content and other components of the photosynthetic machinery and Calvin-Benson-cycle enzymes, including RuBisCO activase, ATP synthase, the oxygen-evolving

Community effects

↓ Net primary productivity
↑ Shifts in composition of species and genotypes

Whole-plant effects

↓ Biomass
↓ Leaf area
↓ Reproductive output
↑ Defense
↑ Senescence

Leaf effects

↓ Photosynthesis
↓ Starch metabolism
↓ Sucrose metabolism
↑ Respiration
↑ Foliar damage
↑ Wax accumulation

Cellular effects

↓ RuBisCO content and activity
↑ Reactive oxygen species scavenging capacity
↑ Protein repair and turnover
↑ Flavonoid biosynthesis

Figure 1

Effects of O_3 on plant processes at the cellular, leaf, whole-plant, and community scales. Arrows indicate directional changes of processes affected by elevated [O_3].

subunit of photosystem II, aldolase, phosphoglycerate kinase, and NADP-glyceraldehyde-3-phosphate dehydrogenase (1, 133). These decreases in primary metabolism at the cellular and leaf level are in part responsible for reductions in leaf area, which in turn reduce ecosystem NPP (**Figure 1**).

Supplemental Material

In addition to fixing less CO_2, plants growing in elevated [O_3] commonly have higher

rates of mitochondrial respiration. This has been observed in numerous crops, including soybean (60), wheat (22), rice (75), and bean (*Phaseolus vulgaris*) (6), as well as several tree species, including Scots pine (*Pinus sylvestris*) (85), beech (*Fagus sylvatica*) (87), and aspen (*Populus tremuloides*) (83, 152). However, at the cellular level, specific metabolic changes resulting from growth in elevated [O_3] are only beginning to be elucidated. In soybean, a negative correlation between [O_3] and transcript abundance of cytosolic ATP-citrate lyase and mitochondrial alternative oxidase 2b (AOX2b) was observed (60). Both of these changes reprogram mitochondrial metabolism to sustain increased rates of respiration, potentially needed for O_3 detoxification and repair of cellular damage. However, a more thorough flux analysis through the tricarboxylic acid (TCA) cycle is needed to identify the control points affected by elevated [O_3].

Sources of Carbon Lost to Indirect Ozone Effects

In addition to decreased carbon availability from O_3-mediated changes in primary metabolism, plant carbon balance is further impacted by indirect costs associated with the detoxification needed to counter the ROS increase generated by O_3. Although the dissolution chemistry of O_3 in the apoplast is not completely understood, the ability of the apoplast to quench ROS generated from O_3 depends upon the concentration of radical-scavenging metabolites and enzymes in the apoplast, the rate of their reactions with O_3, and the rate of regeneration of the reduced compounds (97). The importance of apoplastic ascorbate in providing protection against O_3 damage has been documented (32, 58). However, defense compounds—including numerous flavonoids and volatile terpenoids—also increase following O_3 exposure (80, 163). O_3 stimulates the deposition of epicuticular wax (118), which is composed of very-long-chain fatty acids 28–32 carbons in length. Foliar damage often occurs as a result of the oxidizing effect of

O_3, leading to increased protein turnover (17). Leaf longevity studies have also shown that senescence is induced by elevated [O_3] and represents lost opportunity for carbon gain (117). These metabolic changes can alter source-sink relations, with reduced root biomass commonly reported following chronic O_3 exposure (7, 49). All of these responses to O_3 have an energetic cost to the plant that contributes to the overall decrease in growth and biomass (10).

Measuring and utilizing the direct and indirect O_3 costs at the cellular, leaf, and whole-plant level to accurately predict changes in NPP at the ecosystem level are complicated by a number of factors. First, O_3 gradients vary through a forest canopy (82, 90, 121), with reductions in mean hourly [O_3] of up to 47% at the forest floor (90). Second, tree and leaf age influences the magnitude of the O_3-mediated decrease in photosynthesis. In black cherry (*Prunus serotina*) (164) and beech (70) trees, the decrease in carbon assimilation in older leaves was greater than in young leaves. Finally, O_3 has been shown to affect sun and shade leaves differently, with different ecological types responding in an opposite manner. For example, in shade-tolerant beech and sugar maple (*Acer saccharum*) trees, photosynthesis was more severely decreased in shade-grown leaves (87, 142); however, in hybrid poplar (*Populus* sp.), which is shade intolerant, the largest decrease was in the sun leaves (142, 144). These considerations will need to be factored into future attempts at modeling NPP changes in response to elevated [O_3], making accurate predictions at the ecosystem scale much more challenging.

OZONE EFFECTS ON PLANT PRODUCTIVITY

Effects of Ozone on Crop Production

The NCLAN and EOTC experimental campaigns (discussed above) provided critical information about DRs that enabled regional and global economic projections of O_3 effects on crop yields. More recently, Free Air CO_2 Enrichment (FACE) technology, which avoids

the artifacts caused by enclosed chambers, has also been used to study the effects of increased [O_3] (~25%–50% above current ambient concentrations) on soybean (21, 35, 109, 110), wheat (165), and rice (114, 135). These experiments use the same technology originally developed to enrich vegetation with CO_2 (95). Briefly, an O_3 FACE plot consists of an approximately circular area (~14–20 m in diameter) surrounded by a ring of pipes that release air enriched with O_3 just above the top of the crop canopy. Wind direction, wind velocity, and [O_3] are measured in real time at the center of each plot, and this information is used by a computer-controlled system to adjust the O_3 flow rate, controlled by a mass-flow control valve, to maintain the target elevated [O_3]. The elevated O_3 treatments in the recent FACE experiments are typically within a range currently experienced in polluted areas (daytime seasonal average of 54–75 ppb). Therefore, these experiments provide a useful comparison for the modeled estimates described above as well as a tool for exploring the potential effects of future [O_3] on crops (see sidebar Chambers Versus FACE).

Loss of net assimilation from both decreased leaf-level photosynthetic rates and significantly decreased leaf area was a common feature of soybean, wheat, and rice crops exposed to elevated [O_3] in the field (35, 47, 109, 114). In soybean, the coupling of lower stomatal conductance and reduced leaf area index at elevated [O_3] resulted in a 10% decrease in canopy evapotranspiration, which

CHAMBERS VERSUS FACE

Only a limited number of FACE studies have investigated the influence of crops grown under elevated O_3, and these studies have been confined to three crops in two locations (soybean in the United States and wheat and rice in China). As such, the concentration-response functions that are necessary to perform regional estimates of yield, production, and economic loss owing to O_3 are based primarily on data from field chamber experiments. Concern has been raised that the chamber environment modifies plant response to O_3 (37), with environmental differences between the chamber and the open air either ameliorating or exacerbating the effects of elevated O_3 (94). Comparisons of FACE results against global modeling studies (151) suggest that, if anything, chamber studies would tend to underestimate the yield losses found in the FACE experiments, though the importance of differences in O_3 sensitivity among crop genotypes and years is apparent. Ultimately, such comparisons show that there is a need for more FACE experiments to reduce the uncertainty in future estimates of loss in crop productivity. Ideally, these should be conducted in a range of locations and cover different cropping and management systems (126).

has implications for the terrestrial hydrological cycle (19). The modest increase in [O_3] in the FACE experiments significantly and consistently reduced yield in soybean, wheat, and rice (**Table 1**). For soybean and wheat, decreased seed and grain mass was largely responsible for the yield losses. In rice, however, there was little effect of O_3 on grain mass; rather, O_3 decreased spikelet number per panicle

Table 1 Synthesis of recent Free Air CO_2 Enrichment (FACE) experiments of ozone effects on crops

Crop	Ambient ozone (ppb)	Elevated ozone (ppb)	Grain/seed yield response	Grain/seed weight	Other yield parameters
Rice[a]	42–45	54–59	−15% to −18% (hybrid); −8% (inbred, NS)	NS (hybrid); −4% to −5% (inbred)	Spikelets per panicle (−16%)
Soybean[b]	50–62	63–75	−15% to −25%	−8% to −15%	Pods per plant (−17%)
Wheat[c]	45–47	57–58	−10% to −35%	−14% to −25%	

Ambient and elevated ozone treatments are reported as daytime 8-h means. NS, not significant.
[a]Data from Shi et al. (135).
[b]Data from Morgan et al. (110).
[c]Data from Zhu et al. (165).

(**Table 1**). This is in contrast to many chamber studies reporting that O_3 decreased individual grain mass in rice (3).

A key finding from all of the FACE experiments and other recent open-top chamber experiments is that there is genotypic variability in O_3 sensitivity (21, 25, 135, 165), suggesting that there is potential to breed for O_3 tolerance. Another key finding from the soybean studies is that recently released germplasm is not more tolerant than older germplasm previously tested in the NCLAN experiments (21). In wheat, modern germplasm appears to be more sensitive to O_3 than older germplasm, in part based on higher stomatal conductance in the modern lines (120). Therefore, there is a need to identify and exploit potential O_3-tolerant germplasm. Although there have been efforts to understand the genetic basis for variability in crop tolerance to O_3, and quantitative trait loci associated with O_3 tolerance in rice have been identified (55, 56), there is still little if any industrial effort to breed for O_3 tolerance in any crop (5, 23). This is likely due to a general lack of awareness of O_3 effects on crop production and the variability in $[O_3]$ over time and space, which challenges efforts to screen for O_3 tolerance in a wide pool of germplasm.

Current estimates for global crop yield losses are determined by linking O_3-crop yield response functions defined from the NCLAN and EOTC campaigns to global chemistry transport models that predict hourly $[O_3]$ over the globe. Outputs from these models predict current yield losses ranging from 3% to 5% for maize, 6% to 16% for soybean, 7% to 12% for wheat, and 3% to 4% for rice, representing economic losses of $14 billion to $26 billion (151). Globally, there are a number of agricultural production areas that are vulnerable to increasing O_3 pollution. The Midwest "Corn Belt" in the United States produces 40% of the world's corn and soybean crops, and this region is already potentially losing 10% of its soybean production to O_3 (50, 146). In the United States as a whole, agronomic crop loss to O_3 is estimated to range from 5% to 15%, with an approximate cost of $3 billion to $5 billion

annually (49) owing to the O_3 sensitivity of a number of important crop species grown in North America, including potato (*Solanum tuberosum*), bean, barley (*Hordeum vulgare*), canola (*Brassica napus*), grape (*Vitis vinifera*), soybean, wheat, and rice (for recent reviews, see 23, 45). In Europe, crop losses to O_3 estimated for 23 crops in 47 countries was €6.7 billion per year ($9.6 billion) based on year 2000 emissions (72). The negative effects of O_3 on crop production in Asia and Africa may have even greater relevance for food security because a large proportion of grains are consumed locally and the economies are centered upon agriculture (33). Significant production losses to O_3 are predicted to be occurring in the Indo-Gangetic Plain, one of the most important agricultural regions in the world, indicating that O_3 may be an important contributing factor to the yield gap that currently exists across much of Asia (40). A recent comparison of the O_3 response of Asian and North American crops and cultivars also showed that Asian lines were more sensitive to O_3 than their North American counterparts (40). Because previous modeling studies have relied on North American or European DRs to assess the yield losses caused by O_3, current estimates for Asia may also be significantly too low (40). This is of even greater concern given the results of recent analyses suggesting that there is little potential for crop management practices to adapt to rising $[O_3]$ (140). There is much less O_3 monitoring on the African continent, and the O_3 response of many important African crops has not been tested; therefore, there is a critical gap in knowledge about the effects of current $[O_3]$ on African crop production (130).

Effects of Ozone on Forest and Grassland Productivity

Forest vegetation and soils store more than 50% of terrestrial carbon (36), and the negative effects of O_3 on forest productivity have implications for the global carbon cycle and climate change (44, 138). Recent meta-analyses

comparing northern temperate trees exposed to current ambient $[O_3]$ with those exposed to charcoal-filtered air suggest that O_3 is currently decreasing net tree photosynthesis by 11% (161) and tree biomass by 7% (162). A limitation of extrapolating these data to mature forests is that the estimates are based largely on individual young trees growing in a non-competitive environment, and extrapolation of results from seedlings may not be appropriate for predicting the response of mature trees and forests to O_3 (27, 112).

A FACE experiment similar to the ones described above for crops has also been used to investigate how elevated $[O_3]$ affects northern temperate forest communities (84). Increasing tropospheric $[O_3]$ from daily seasonal means between 33–39 ppb and 49–55 ppb caused significant reductions in the total biomass of aspen (23%), aspen–paper birch (*Betula papyrifera*; 13%), and aspen–sugar maple (14%) communities but did not alter biomass partitioning (86). The Aspen FACE experiment also showed significant variation in O_3 tolerance among aspen genotypes, with the most sensitive genotype ultimately disappearing from the canopy by the end of the 11-year experiment (91). Exposure of these communities to both elevated $[CO_2]$ and elevated $[O_3]$ demonstrated that O_3 has the potential to offset the positive effects of elevated $[CO_2]$ (83). Although this FACE experiment in Rhinelander, Wisconsin, in the United States is the only experiment that essentially exposed a forest to increased $[O_3]$ from seedling establishment through to maturity, it still largely captured the O_3 response of immature, rapidly growing trees.

An alternative experimental approach recently used to understand the effects of current fluctuations in O_3 on growth of mature trees coupled high-resolution measurements of stem growth, sap flow, and soil moisture to high-resolution O_3 monitoring (103). High-$[O_3]$ episodes (i.e., daily maximum values >100 ppb) caused a periodic disturbance to growth patterns that was attributed to amplification of diurnal patterns of water loss. These daily events culminated into large

seasonal losses in stem growth of 30%–50% for most species investigated (103). Another experimental approach, using a chamberless, open-air exposure system, was used to investigate the effects of O_3 on mature sugar maple trees (143, 144). Sunlit and shaded branches were exposed to double ambient $[O_3]$ (95 ppb on average), which reduced photosynthesis and impaired stomatal function. This experiment was among the first to investigate the effects of elevated $[O_3]$ on mature branches, but it was limited to individual branches on a tree. A different open-air canopy O_3 fumigation system was established in the Kranzberg forest in Germany to investigate the response of mature beech and spruce (*Picea abies*) trees that were approximately 60 years old and located in a 28-m closed canopy (101). This system consisted of 150 Teflon tubes vertically suspended approximately 0.5 m from the foliated canopy of the mature beech trees. O_3 was emitted through pressure-calibrated capillary outputs, and trees were accessed via scaffolding and a research crane. After 8 years of O_3 exposure, beech stem productivity was reduced by 44% (124). In 2003, drought-induced stomatal closure uncoupled O_3 uptake from O_3 exposure, and drought rather than O_3 limited tree growth (101). Although these open-air experiments largely confirm the data from decades of controlled-environment studies, they also revealed that environmental conditions, competition, ontogeny, and plant history can alter tree responses to O_3 and decouple O_3 exposure from O_3 uptake (101). Therefore, there is a critical need for research investigating how O_3 will interact with other environmental changes and impact forest productivity.

Grasslands are highly diverse, multispecies communities with a wide range of productivities. Therefore, predicting the response of grasslands to O_3 is complex, dependent upon both the sensitivities of individual species and the mutualistic interactions, competitive interactions, and specific microclimatic conditions, which may influence individual O_3 responses. Although experiments have documented that elevated $[O_3]$ decreases grassland productivity

(14, 153), other experiments with established temperate (154), calcareous (141), and alpine grasslands (15) have shown that the NPP of these systems is relatively resilient to rising [O_3]. Species have also been shown to respond differently to O_3 depending on competition (134), and O_3 can have carryover effects on growth and overwintering of grassland species (67). O_3 also causes more subtle changes in carbon assimilation, leaf longevity, and biomass partitioning of grassland species, suggesting that grassland productivity may decline in the longer term in response to O_3 (33). The vast majority of research investigating grassland responses to O_3 comes from Europe, with little experimentation done in the United States, even less in Asia, and none in the tropics. Thus, compared with trees and crops, much less is known about how grasslands are impacted by [O_3].

As previously described, leaf-level O_3 response data can be combined with ecosystem models to predict O_3 effects on canopy- and stand-level processes. Such modeling studies estimate that O_3 is currently reducing temperate forest biomass accumulation and NPP by ~1%–16% (44, 112, 129). A mechanistic model of plant-O_3 interactions was implemented into the Hadley Centre land-surface model and run with O_3 scenarios from the Met Office Lagrangian tropospheric chemistry transport model (132) to estimate the impact of current [O_3] on global NPP (138). This model defined five plant functional types—broad-leaved trees, conifers, C_3 grasses, C_4 grasses, and shrubs—and uses a different O_3 sensitivity function for each plant functional type. Using scenarios of both "lower" and "high" plant sensitivity to O_3, the model estimated that current [O_3] may be reducing NPP over parts of North and South America, Europe, Asia, and Africa by 5%–30% (**Figure 2**), which broadly agrees with estimates from recent meta-analyses (66, 162). This model has also been used to estimate future impacts of O_3 on global productivity, and the results suggest that O_3 may offset potential gains in global gross primary productivity from rising atmospheric CO_2 by 18%–34% (138). These
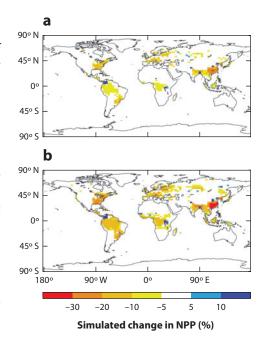

Figure 2

Simulated percentage change in net primary productivity between 1901 and 2002 due to O_3 effects and considering changes in atmospheric CO_2 for (*a*) "lower" and (*b*) "high" O_3 plant sensitivity.

results were overlaid with the World Wildlife Foundation Global 200 priority conservation areas to assess future threats of O_3 to biodiversity (126). Key biodiversity areas in south and east Asia, central Africa, and Latin America were identified as being at risk from elevated [O_3] (**Figure 3**).

Although the outputs from these modeling exercises offer the only global estimates of O_3 effects on NPP and associated impacts on ecosystem properties and services, there are limitations to these findings. Importantly, the O_3 response of the five plant functional types was considered to be representative for all ecosystems, whereas there is almost no information about the O_3 sensitivity of tropical species (138). Furthermore, a limited number of natural species have been investigated to define the O_3 sensitivity functions (66). The model also did not include many of the interactions that could alter [O_3] in the leaf and canopy
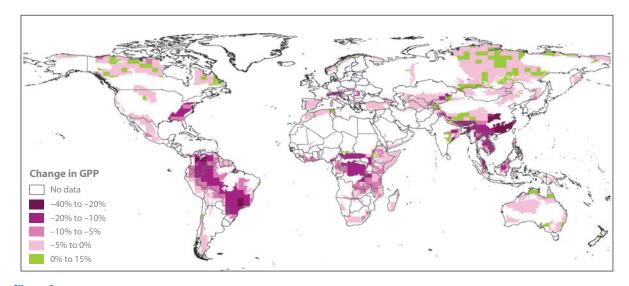
Figure 3

Global assessment of the projected percentage changes in gross primary productivity (GPP) due to O_3 under the Intergovernmental Panel on Climate Change A2 scenario in 2100 within the World Wildlife Foundation Global 200 priority conservation areas. Adapted with permission from the Royal Society (126).

boundary layer, including VOCs or soil NO_x. Finally, the model did not include a direct effect of O_3 on stomatal functioning, which may be needed to accurately characterize plant responses under conditions of water limitation (106). Still, the models support experimental findings that O_3 has had a significant negative impact on terrestrial NPP since the Industrial Revolution, which has important implications for terrestrial carbon storage and global radiative forcing (138).

INTERACTIONS, FEEDBACKS, AND CLIMATE CHANGE

O_3 is unlikely to be the only stress that plants experience during their growth and development, especially given that O_3 formation occurs in polluted regions and forms during periods of hot, dry, sunny weather. Empirical data have shown that plant response to O_3 is modified under other aspects of environmental change that stress plant systems, including other pollutants, atmospheric $[CO_2]$, temperature, precipitation (or soil moisture availability),

and nitrogen availability. Moreover, plant responses to O_3 and alterations to natural emissions of O_3 precursors from plant systems have the potential to feed back on tropospheric $[O_3]$, with implications for climate change. Below, we outline key interactions between O_3 and these other stressors and discuss feedbacks to the atmosphere and climate system.

Because fossil fuel combustion is an important source of NO_x and sulfur dioxide (SO_2) as well as O_3 precursors, these species have a tendency to co-occur as a cocktail of atmospheric pollutants (42). Past studies conducted in Europe and North America investigated plant response to a limited mixture of different, mostly gaseous, pollutants, with a tendency to focus on interactions between SO_2, nitrogen dioxide (NO_2), and O_3 because these represented the combination of atmospheric pollutants most likely to occur in these regions. Over the past 20 years the number of such studies has declined, driven largely by changes in the atmospheric pollutants in Europe and North America. However, the results of such studies may have heightened relevance for

Asia and other rapidly industrializing regions where emission controls are not yet fully implemented. Unfortunately, because responses to pollutant mixtures are highly variable depending on plant species, environmental conditions, pollutant combinations, exposure profiles, and seasonality, plant responses cannot be readily inferred, even in general terms (16, 42). As modeling approaches become more sophisticated, it may become possible to address pollutant combinations; however, such efforts will perhaps be better targeted toward improving our understanding of multiple stresses (e.g., pollutant combinations and environmental conditions) that affect not only ecosystem response but also atmospheric composition, with consequences for climate change.

The interactive effects of O_3 and atmospheric $[CO_2]$ on plants have received much attention (reviewed by 57), although understanding is far from complete. Increased atmospheric $[CO_2]$ reduces stomatal conductance (4), which subsequently decreases O_3 flux into plants (49). A recent modeling analysis concluded that despite substantially increased future $[O_3]$ in central and southern Europe, the flux-based risk of O_3 damage to vegetation was unchanged or decreased at sites across Europe, mainly as a result of projected reductions in stomatal conductance under rising $[CO_2]$ (88). Such reductions in O_3 uptake would also lead to increased atmospheric $[O_3]$ in the boundary layer; in fact, a doubling of $[CO_2]$ was estimated to increase $[O_3]$ over parts of Europe, Asia, and the Americas by 4–8 ppb during the crop growing season (131). However, the relationship between stomatal conductance and $[CO_2]$ may prove to be more complex than is often assumed, and elevated $[CO_2]$ may not completely alleviate the adverse effect of O_3 (148). At the leaf level, elevated $[CO_2]$ largely protected soybean from elevated $[O_3]$ (18); however, elevated $[CO_2]$ may not always protect plants from changes in senescence and allocation caused by elevated $[O_3]$ (49). There is evidence from long-term field experiments that O_3 can significantly alter carbon cycling and reduce the increase in forest soil carbon sequestration caused by elevated $[CO_2]$ (83, 96). However, the scant experimental data on the long-term effects of O_3 on soil carbon fluxes in a range of ecosystems is a major limitation to understanding the impacts of O_3 on global carbon fluxes (7, 10). Atmospheric $[CO_2]$ and $[O_3]$ also have the potential to alter nitrogen cycling in forest ecosystems through influences on plant growth and litter production. Generally, CO_2 stimulates photosynthesis, leaf, and root litter production, whereas O_3 damages photosynthetic tissues and accelerates leaf senescence. The interactions between O_3, CO_2, and nitrogen are complex and dependent on plant and soil microbial processes, which feed back on nitrogen availability (73).

As atmospheric $[CO_2]$ increases in the future, the global climate will change. In particular, temperature will increase and precipitation will change, and both are important determinants of stomatal conductance, NPP, and O_3 uptake. As such, reduced stomatal conductance that occurs in response to elevated $[CO_2]$ may enhance plant water-use efficiency, which could help to partly alleviate the effects of reduced rainfall (92). Increased water stress in a warmer climate may also decrease sensitivity to O_3 through reduced uptake (57); however, O_3-induced damage to stomatal functioning (99, 106, 159, 160) might confound this effect. Understanding how combinations of increased temperature, drought, and O_3 might interact to influence plant transpiration and hence water balance is complicated by our limited knowledge of the processes involved (9). One of the few examples of observational data investigating responses to stress combinations is that collected for a mixed deciduous forest in eastern Tennessee, United States (103). These data suggest an increase in water use under warmer climates with high $[O_3]$, with subsequent growth limitations for mature forest trees and implications for the hydrology of forest watersheds (104).

Higher temperatures and altered precipitation can also affect O_3 formation through alterations to natural emissions of O_3 precursors. For example, isoprene emissions are known to

depend strongly on plant species, temperature, light intensity, season, and leaf age (64). Thus, under higher temperatures, isoprene emissions would be expected to change, thereby impacting atmospheric $[O_3]$ (125). Atmospheric $[CO_2]$ can also directly affect isoprene emissions, although CO_2-induced changes in leaf area can compensate for the decrease such that canopy isoprene emissions do not differ from ambient $[CO_2]$ (123). Changes in the global distribution of vegetation and in particular future biofuel plantations could also affect natural emissions such as isoprene (158); modeling studies have suggested that inclusion of such changes is important for our understanding of historical and potential future changes in surface $[O_3]$ (20, 132). It is clear that changes in temperature and precipitation that accompany rising atmospheric $[CO_2]$ have the potential to alter O_3 production and deposition rates as well as plant responses to O_3. There is also limited evidence to suggest that O_3 can affect CH_4 emissions from peatlands, possibly through O_3 causing plants to alter substrate availability to soil microbes or causing changes in transport of CH_4 through vascular plants with aerenchymatous tissue (145). The implications of such O_3 effects on CH_4 emissions could provide important feedbacks because CH_4 emissions themselves contribute significantly to predicted increases in global background $[O_3]$ (157).

Finally, as the climate changes, so can the incidence and distribution of pests and diseases; because studies have also shown that O_3 can mediate such impacts, either by causing toxicity to the secondary stress or by affecting the abundance and quality of the host plant (51, 57, 58), interactions between climate and O_3 on the prevalence of such secondary stresses should also be considered. Interactions may also occur with increased nitrogen deposition to nitrogen-limited ecosystems because insect herbivores are frequently limited by nitrogen availability. Additionally, rising atmospheric $[CO_2]$ may increase plant productivity at the expense of foliar nitrogen concentrations and may increase production of carbon-based allelochemicals, both of which reduce the quality

IPCC SPECIAL REPORT ON EMISSIONS SCENARIOS

The IPCC Special Report on Emissions Scenarios (76) describes four scenario families (A1, A2, B1, and B2) that explore alternative development pathways; these pathways include a wide range of demographic, economic, and technological driving forces of greenhouse gas emissions. The A1 scenario assumes a world of very rapid economic growth, a global population that peaks in midcentury, and rapid introduction of new and more efficient technologies; A2 describes a very heterogeneous world with high population growth, slow economic development, and slow technological change; B1 describes a convergent world, with the same global population as A1 but more rapid changes in economic structures toward a service and information economy; and B2 describes a world with intermediate population and economic growth, emphasizing local solutions to economic, social, and environmental sustainability (77).

of the host plant (51). Unfortunately, data for specific pest, disease, and plant species competition interactions are often controversial (57), complicating efforts to project parasite-host interactions under future environmental change.

There are large uncertainties about future regional and global $[O_3]$, largely associated with uncertainties in precursor emissions. Emissions scenarios are based on a range of socioeconomic story lines and on assumed levels of technology adoption and O_3-relevant legislation (see sidebar IPCC Special Report on Emissions Scenarios). **Figure 4** shows the decrease in the carbon stored on land (in vegetation and soils) as O_3 pollution levels increase from 1900 levels to projected 2050 levels. The solid lines show significant decreases in carbon stored into the twenty-first century with a high-emissions A2 scenario, with no restrictions on pollutant emissions [Intergovernmental Panel on Climate Change (IPCC) Special Report on Emissions Scenarios (SRES) A2] (138). However, legislation to control air quality is in place in many countries. These measures (which are designed to protect both people and crops) will slow down the damage. The dashed lines are much flatter, and show
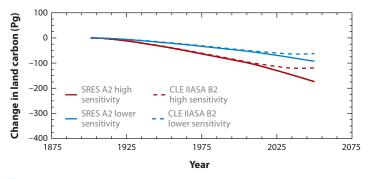
Figure 4

Temporal changes in land carbon storage for "lower" (*blue*) and "high" (*red*) plant sensitivities to O_3. These results were obtained from model simulations using a fixed industrial [CO_2] and climate. Spatially explicit [O_3] fields were derived from the STOCHEM atmospheric chemistry model (132) and used to drive the modified JULES land-surface scheme offline (30). The figure includes two emissions scenarios, one with enactment of current pollution controls [current legislation scenario (CLE) International Institute for Applied Systems Analysis (IIASA) B2] and one without pollution controls [Intergovernmental Panel on Climate Change Special Report on Emissions Scenarios (SRES) A2] (for more details, see References 138 and 126, respectively). STOCHEM generated monthly [O_3] fields for preindustrial, present-day, and future periods. These data points were linearly interpolated to provide annual data over the simulation period. A detailed description of the experimental design is given in Reference 138.
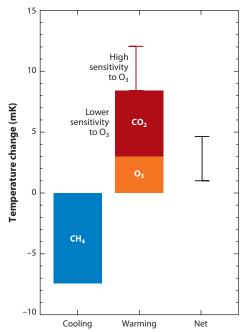

Figure 5

Temperature changes following a 20% step increase in man-made NO_x emissions (31). Estimates were calculated using simple relations between radiative forcing and temperature. The NO_x emissions cause CH_4 destruction (cooling, *blue bar*) and increased [O_3] (warming, *orange bar*), which without including damage to plants produces an overall cooling. However, on inclusion of O_3 damage to plants and subsequent decreases in photosynthesis and net primary productivity, the extra CO_2 remaining in the atmosphere (*red bar*) leads to an overall warming (*third column*). The red bar shows the effects when assuming a "lower" sensitivity of plants to O_3. The red whisker shows an additional effect if plants are assumed to have a "high" sensitivity and so represents the uncertainty in our understanding.

the improvement expected when following a lower-emissions scenario [current legislation scenario (CLE) International Institute for Applied Systems Analysis (IIASA) B2], assuming full adherence to currently enacted air quality legislation (126). In addition to producing O_3 and indirectly increasing atmospheric [CO_2], air pollutants can act to increase or decrease the amount of atmospheric CH_4, which is a potent greenhouse gas. From an O_3 air quality point of view, the most effective emissions to control are those of NO_x. Previous reports (e.g., 77) found that NO_x emissions, on balance, cool the climate. Therefore, reducing NO_x emissions would benefit air quality but warm the climate. However, when the O_3 damage to plants is considered, additional CO_2 remains in the atmosphere because of lower photosynthetic rates (31). Thus, the effect of NO_x emissions is to increase climate warming from a combination of the warming potential of O_3 and CO_2 (**Figure 5**). This now suggests that reducing NO_x emissions would benefit

both air quality and climate. Other pollutants, such as non-CH_4 VOCs, also produce O_3. For these, the chemical effects are all warming, and the O_3-plant-damage effect further enhances this. Modeling the effects of tropospheric O_3 on terrestrial ecosystems along with the other climate-forcing agents—including CO_2, CH_4, N_2O, and aerosols—led to the conclusion that tropospheric O_3 has a relatively large negative effect on NPP but a positive response on surface runoff (i.e., freshwater supply) (74).

KNOWLEDGE GAPS

Currently, only Europe and North America frequently monitor O_3 in rural/remote regions, and in many parts of the world O_3 monitoring is extremely limited, if not nonexistent. An improved understanding of the impact of O_3 on ecosystems (especially grasslands and tropical systems) will aid in assessing the threat that O_3 plays to essential ecosystem services, including food production, carbon sequestration, and freshwater supply. In particular, the global modeling efforts described above consider only a direct effect of O_3 on photosynthesis and an indirect effect on stomatal conductance. More research is needed to determine the circumstances in which chronic O_3 directly impacts stomatal conductance and how to incorporate those situations into global models of ecosystem productivity and hydrology. In addition, the role that climate change will play in enhancing future O_3 formation and deposition needs to be considered within a geographical context. Finally, understanding how O_3 acts in combination with other stressors (e.g., climate change, including heat and drought stress, excessive nitrogen deposition, and high atmospheric aerosol loading) will also be important to fill gaps in our knowledge of where best to target control efforts. The growing interest in O_3 as a short-term climate forcer and the associated human health, arable agriculture, and ecosystem benefits that its reduction might bring make this a pollutant of particular interest for appropriate policy intervention. As such, efforts to control O_3 may benefit from coordinated hemispheric- or global-scale action that is closely integrated with efforts at the regional and local scales.

SUMMARY POINTS

1. O_3 is both a greenhouse gas and a secondary air pollutant causing impacts on climate, human health, and ecosystems. Currently, O_3 is controlled only at the regional and local scales, with controls largely limited to urban areas in Europe, North America, and some parts of Asia.

2. Extensive experimental and modeling studies have highlighted the deleterious effects of surface O_3, which include reductions in crop yields, reduced forest biomass, and altered species composition of grasslands and seminatural vegetation.

3. The effects of O_3 on vegetation can feed back to the climate system through alterations to carbon sequestration.

4. Climate change itself can alter natural emissions of O_3 precursors, some of which are also radiative forcing agents.

5. The complex set of interactions and feedbacks emphasizes the need to take O_3 pollution seriously at local, regional, and hemispheric scales. More efforts are required to improve our understanding of O_3 pollution biology such that appropriate emissions control measures can be introduced to limit O_3 impacts on ecosystem services.

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