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· Invited Expert Review ·

The Ozone Component of Global Change: Potential Effects on Agricultural and Horticultural Plant Yield, Product Quality and Interactions with Invasive Species

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The productivity, product quality and competitive ability of important agricultural and horticultural plants in many regions of the world may be adversely affected by current and anticipated concentrations of ground-level ozone (O_3). Exposure to elevated O_3 typically results in suppressed photosynthesis, accelerated senescence, decreased growth and lower yields. Various approaches used to evaluate O_3 effects generally concur that current yield losses range from 5% to 15% among sensitive plants. There is, however, considerable genetic variability in plant responses to O_3. To illustrate this, we show that ambient O_3 concentrations in the eastern United States cause substantially different levels of damage to otherwise similar snap bean cultivars. Largely undesirable effects of O_3 can also occur in seed and fruit chemistry as well as in forage nutritive value, with consequences for animal production. Ozone may alter herbicide efficacy and foster establishment of some invasive species. We conclude that current and projected levels of O_3 in many regions worldwide are toxic to sensitive plants of agricultural and horticultural significance. Plant breeding that incorporates O_3 sensitivity into selection strategies will be increasingly necessary to achieve sustainable production with changing atmospheric composition, while reductions in O_3 precursor emissions will likely benefit world food production and reduce atmospheric concentrations of an important greenhouse gas.

Key words: climate change; crop; forage; horticultural plant; ozone; product quality; weed; yield.

Ozone (O_3) in the stratosphere provides protection from lethal short-wave solar ultraviolet radiation, but in the troposphere O_3 is both an air pollutant and a greenhouse gas. At current and projected future concentrations it contributes significantly to global warming (Forster et al. 2007). Although O_3 at low concentration is a normal component of the unmodified troposphere, background levels have doubled since pre-industrial times, with current average concentrations ranging from 20 to 45 nL/L (Guicherit and Roemer 2000; Vingarzan 2004). Ozone contributes to warming of the atmosphere by reducing outgoing infrared radiation into space. Positive radiative forcing (heating) from tropospheric O_3 is now estimated with 95% confidence to be 0.25–0.65 W/m^2 (Forster et al. 2007). This accounts for about 25% of the net total radiative forcing (1.6 W/m^2) attributed to human activities since the industrial era began, with long-lived greenhouse gases (CO_2, CH_4, N_2O and halocarbons) contributing most of the remainder (2.63 W/m^2) (Forster et al. 2007). Negative radiative forcing (cooling) due to increased aerosols, and the associated increase in cloud albedo, largely account for the difference between the total positive and net radiative forcing estimates (Forster et al. 2007).

Despite air quality regulations intended to limit O_3 pollution, current ground-level O_3 concentrations in a number of countries worldwide can suppress growth and yield of many agricultural and horticultural plants (Emberson et al. 2001; US EPA 2006; Mills et al. 2007). Ozone is the most phytotoxic of the common air pollutants, and its widespread distribution presents a risk for considerable plant damage. Visible foliar injury under ambient conditions is reported from more than 20 countries in Asia, Africa, Australia, Europe, and North and South America (Krupa et al. 2001). Every region of the USA except for sections of the Pacific Northwest and the Northern Great Plains experiences phytotoxic ambient O_3 concentrations periodically during the growing season (US EPA 2006; Tong et al. 2007). In addition, East Asia, India, Pakistan, many countries around the Mediterranean, Europe, parts of Mexico and Brazil are likely experiencing reductions in crop and forage production due to ambient O_3 (Emberson et al. 2001; Wang and Mauzerall 2004; Ashmore 2005; Ren et al. 2007). Emission models of the O_3 precursor, NO_x, in eastern USA, Europe and East Asia imply that 9% to 35% of the world's cereal crops are exposed to seasonal O_3 concentrations that reduce yields by at least a few percent (Chameides et al. 1994). Over 20% of the crop production land in Europe in 2002 was estimated to be at risk for yield losses of 5% or more due to O_3 pollution, not considering effects on grasslands and changes in forage nutritive value (Mills et al. 2007). Modeled ground-level O_3 concentrations combined with an experimentally-derived yield loss function indicated that ambient O_3 reduced US soybean (*Glycine max* (L.) Merr.) production by 10% in 2005 (Tong et al. 2007). Simulations of cumulative O_3 concentrations in China suggested that soybean and wheat (*Triticum aestivum* L.) yields were suppressed by 12% to 19% in 1990 (Wang and Mauzerall 2004). Rice (*Oryza sativa* L.) yields were lowered there by 3% to 5% in 1990, based on estimated seasonal average O_3 concentrations (Wang and Mauzerall 2004). Climate models forecast that areas with the greatest production of peanut (*Arachis hypogaea* L.), rice and soybean, namely China, Japan, India, central Africa, the USA and Indonesia, will continue to experience phytotoxic concentrations of ground-level O_3 in the coming 50 years (Emberson et al. 2001; Wang and Mauzerall 2004; Dentener et al. 2005). Rising NO_x emission rates from increased use of fossil fuels and fertilizers in developing countries will increase these impacts (Chameides et al. 1994). Rising levels of another changing atmospheric constituent, CO_2, will likely moderate the influence of ground-level O_3 on crop productivity (Fuhrer 2003; Fiscus et al. 2005; US EPA 2006; Feng et al. 2008), but eventual impacts of the suite of global climate change variables on yield remain unclear.

Ozone poses a critical threat and a challenging problem to world food security, fiber and timber production, conservation and genetic diversity of natural plant communities (Krupa et al. 2001; Fuhrer and Booker 2003; Ashmore 2005). However, in the USA where research and regulatory activity have taken place since the Air Pollution Control Act of 1955 and the Clean Air Act of 1970 were enacted, considerable uncertainty still remains in attempts to extrapolate results of plant responses to O_3 under experimental conditions to expected responses under ambient conditions (CASAC 2006, http://www.epa.gov/sab/pdf/casac-07-001.pdf). This is true at the local scale, and, for a variety of reasons, even greater uncertainty underlies attempts to extrapolate local results to regional or larger spatial scales. Environmental factors such as temperature, leaf-to-air vapor pressure deficit (VPD_l), soil moisture and solar radiation modulate O_3 uptake by plants and thus influence concentration-response relationships. Genotype and developmental stage also play major roles in determining plant sensitivity to O_3. Research on plant responses to the uptake of O_3 by plant canopies and individual plants (flux) should aid in resolving some of the uncertainties associated with interacting environmental and biological factors (Fuhrer and Booker 2003; Fiscus et al. 2005; Pleijel et al. 2007; Matyssek et al. 2008), but implementation of this approach for assessment and regulatory purposes remains problematic due to the lack of relevant data and the complexity of locally varying input parameters. However, understanding how various factors affect O_3 flux as well as how plants cope with O_3 toxicity are essential for accurate predictions of ambient O_3 impacts on vegetation. There continues to be a critical need to obtain quantitative data on the relationship between O_3 exposure and response of a variety of plant species under ambient and changing climatic conditions, and an equally compelling need for information on biological mechanisms of O_3 responses for development of process models.

In the present study, we focus on the direct and indirect effects of O_3 on agricultural and horticultural plants. These species are essential for food and fiber production, and many have been demonstrated to be sensitive to ambient O_3 concentrations (Heagle 1989; Fuhrer et al. 1997; Mills et al. 2007; Pleijel et al. 2007). Previous reviews have provided detailed examination and interpretation of O_3 effects on crop physiology, reproductive processes and product quality (Heagle 1989; Black et al. 2000; Fuhrer and Booker 2003; Ashmore 2005; Fiscus et al. 2005; US EPA 2006). Our objective is to update and extend some of these analyses. We examine the etiology of O_3 toxicity and its effects on plant development and biomass partitioning, and review various methods used to assess plant responses to O_3. We summarize current estimates of yield impacts and present recent results from experiments with three snap bean (*Phaseolus vulgaris* L.) lines to demonstrate the effect of genetic variability in O_3 sensitivity among otherwise similar genotypes. We show that O_3 often has undesirable effects on yield quality that directly affect seed and fruit chemistry as well as forage nutritive value. We consider examples of O_3 effects on herbicide efficacy and inter-specific competition between crops and weeds as an indication of the complexity of O_3 impacts on agricultural production systems. Our conclusions provide a general assessment of current and future anticipated impacts of ambient O_3 on food production in a changing climate and suggest some research priorities needed to address those issues.

Ozone Toxicity and Developmental Effects

Ozone injures plants mainly following uptake through the stomata in the leaf surface. However, O_3 does not persist in the intercellular spaces of the leaf, but rapidly reacts with water, ascorbate, thiols, phenolics and transition metals in the apoplast to yield reactive oxygen species (ROS) and toxic compounds (Long and Naidu 2002; Fuhrer and Booker 2003). Biogenically-derived oxidative bursts can result from O_3 exposure, which amplify production of ROS (Sandermann 1996; Kangasjarvi et al. 2005). Protein oxidation, ozonolysis of membrane lipids, production of toxic intermediates and altered gene expression result in impaired photosynthesis, stimulated production of ethylene, accelerated senescence and detrimental effects on metabolic processes (Sandermann 1996; Long and Naidu 2002; Fuhrer and Booker 2003; Kangasjarvi et al. 2005; Matyssek et al. 2008). Some of the changes in plant metabolism due to O_3 become manifest in a variety of visible foliar injury symptoms (Krupa et al. 2001), although lowered net photosynthesis (A) and biomass production can also occur without the appearance of visible injury (Reich 1987).

Antioxidant metabolism is considered to be a critical component in plant responses to O_3 stress. Activities of antioxidant enzymes such as peroxidase and glutathione reductase are often increased by O_3 (Dixon et al. 1996; Burkey et al. 2000; Chen and Gallie 2005; Cheng et al. 2006; US EPA 2006). In addition, the antioxidant compound most studied in this regard is ascorbic acid (vitamin C). Deficiencies in ascorbic acid concentrations have been linked to enhanced O_3 sensitivity in *Arabidopsis* mutants (Conklin et al. 1996), transgenic tobacco (*Nicotiana tabacum* L.) (Chen and Gallie 2005) and in wildflowers that naturally accumulate low levels of ascorbate (Burkey et al. 2006). Transgenic tobacco with lowered ascorbate redox states exhibited increased sensitivity to O_3 as well (Sanmartin et al. 2003; Chen and Gallie 2005). Overexpression of dehydroascorbate reductase or monodehydroascorbate reductase in transgenic tobacco lines resulted in increased ascorbate availability, higher ascorbate redox state and improved tolerance to O_3 (Chen and Gallie 2005; Eltayeb et al. 2007). However, leaf content of antioxidant compounds such as ascorbic acid, glutathione and vitamin E were not consistently good predictors of O_3 sensitivity (Wellburn and Wellburn 1996; Burkey et al. 2000). There is evidence that cellular localization of antioxidants, particularly in the leaf apoplast where O_3 responses originate, may be more important than total antioxidant content. Leaf apoplast ascorbic acid content varies significantly across species and in certain cases appears to mediate O_3 responses (Burkey et al. 2003), although apoplast compounds other than ascorbate may also be involved (Fuhrer and Booker 2003; Cheng et al. 2006). Ozone-scavenging reactions by biogenically-produced volatile organic compounds might be protective against O_3 injury (Fiscus et al. 2005; Loreto and Fares 2007). Given the diversity of plant metabolism, it is reasonable to expect that plants have a variety of genetic and metabolic mechanisms for coping with O_3 stress. Depending on the species and exposure conditions, these systems may have the capacity to mediate or suppress O_3 effects or to become overwhelmed to the point where injury responses are initiated.

Suppressed carbon assimilation and growth are typical responses of many plants to O_3 (Reich 1987), caused in large part by decreased Rubisco activity and content (Pell et al. 1997; Reid and Fiscus 1998; Long and Naidu 2002; Fiscus et al. 2005). For example, seasonal average A and the maximum rate of carboxylation ($V_{c,max}$), an indicator of Rubisco activity, declined by 40% in an O_3-sensitive snap bean line (S156) following treatment with 60 nL/L O_3 (12-h daily average) in outdoor controlled-environment chambers (Table 1) (Flowers et al. 2007). Yield suppression correlated with reduced A, although early leaf senescence likely contributed to the effect as well. Lower Rubisco activity is attributed to both decreased mRNA transcripts for the protein and decline in content of the enzyme (Pell et al. 1997; Fiscus et al. 2005). Oxidation of proteins may be involved too. Protein carbonylation, a targeted, oxidative process that leads to a loss of protein function, increased in soybean leaves following chronic O_3 exposure (Qiu et al. 2008). Studies with bean found that carbonylation of the Rubisco small subunit increased with increasing O_3 concentrations from 54 to 108 nL/L over 7 h/d for up to 30 d and was always accompanied by visible foliar injury (Kanoun et al. 2002; Leitao et al. 2003). The mechanisms involved in increased carbonylation are not well

Table 1. Seasonal average net photosynthesis (*A*) and the maximum RuBP-saturated rate of carboxylation ($V_{c,max}$) in O_3-sensitive (S156) and -tolerant (R123, R331) snap bean lines

12 h Mean	A (μmol/m^2 per s) Genotype			$V_{c,max}$ (μmol/m^2 per s) Genotype		
(O_3) (nL/L)	S156	R123	R331	S156	R123	R331
0	27.0^{aA}	21.8^{aB}	23.2^{aB}	159.7^{aA}	129.5^{bB}	124.8^{aB}
15	26.6^{aA}	23.4^{aA}	23.1^{aA}	148.2^{abA}	140.2^{abA}	128.8^{aA}
30	23.5^{aA}	20.7^{aA}	22.0^{aA}	125.9^{bA}	121.4^{bA}	110.6^{aA}
60	16.6^{bB}	22.2^{aA}	19.7^{aAB}	90.4^{cB}	138.8^{aA}	112.5^{aB}

Plants were treated from emergence to physiological maturity with four different levels of O_3 in outdoor controlled environment chambers in Raleigh, North Carolina (Flowers et al. 2007). Means followed by the same letter are not statistically different at the 0.05 level. Lower case letters separate means by (O_3) within each genotype. Upper case letters separate means by genotype within a given (O_3).

understood, but might be related to a secondary oxidative burst mediated by membrane NAD(P)H oxidases in response to O_3 (Kanoun et al. 2002). Increased protein carbonylation might thus be involved in the decline in Rubisco activity and *A* due to O_3.

One of the most common effects of O_3 is to promote leaf senescence (Pell et al. 1997). Senescence is a normal process, proceeding from older to younger tissue, though the process is accelerated by O_3 (premature aging). In tomato (*Lycopersicon esculentum* Mill.), for example, where a clear progression of senescence is normally observed, elevated O_3 accelerated the course of that senescence, as shown by increased loss of chlorophyll from older, more sensitive leaves lower in the canopy (Figure 1). Soybean yield loss at elevated O_3 in the open-air SoyFACE experiment was attributed in large part to accelerated senescence, as evidenced by a more rapid loss of leaf dry mass and leaf number during the pod-fill stage compared with plants grown in ambient air (Morgan et al. 2006). Accelerated senescence reduces canopy photosynthesis during reproductive growth and thus can limit fruit and seed yields.

Reduced phloem loading and lower carbon allocation to sink tissues due to O_3 exposure also contribute to suppressed biomass production and yield (Grantz and Farrar 2000). A particularly significant physiological effect in many plant species is reduced biomass allocation to roots (Cooley and Manning 1987; Miller 1988; Andersen 2003; Grantz et al. 2006; Feng et al. 2008), which could be related to decreased net assimilation and early senescence in lower canopy leaves that are the main source of photosynthates for root growth (Cooley and Manning 1987; Grantz et al. 2006). Decreased allocation to roots might also result from increased demand for carbohydrates in the shoot needed to support higher rates of maintenance respiration (Miller 1988). Reduced carbon flow to the roots and suppressed biomass production in general have significant consequences for nutrient uptake, soil organic matter content and for plant vigor and resilience to multiple stresses (Andersen 2003; Fuhrer and Booker 2003). Although root system development in many crops is substantially reduced by O_3 exposure of the shoot (Grantz et al. 2006) this may be expressed differently in plants with different reproductive strategies (Figure 2). In tomato, for example, where fruits are borne on aerial branches, carbohydrate allocation below ground is reduced (Shrestha and Grantz 2005). In contrast, in yellow nutsedge (*Cyperus esculentum* L.), a common weed species that reproduces mostly by vegetative tubers borne on underground stems (rhizomes), O_3 did not cause a decline in allocation below ground (Shrestha and Grantz 2005). Ozone pollution thus may influence competition relationships

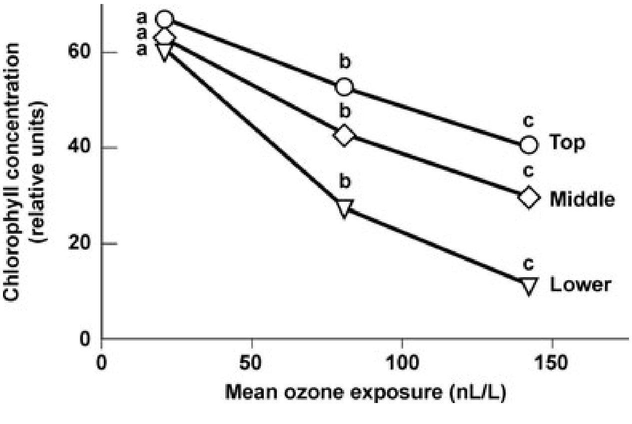

Figure 1. Ozone acceleration of the normal progression of canopy senescence in tomato, shown as declining leaf chlorophyll content (relative units) with increasing O_3 exposure in leaves of various ages (after Shrestha and Grantz 2005). Values within each line associated with different letters differ at $P \leq 0.05$.

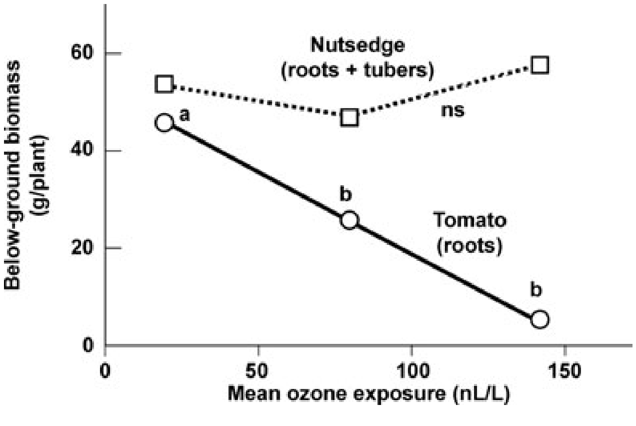

Figure 2. Differential effects of O_3 exposure on biomass allocation below-ground in a sexually reproducing species, tomato, and a vegetatively reproducing species, nutsedge (after Shrestha and Grantz 2005). Values within each line associated with different letters differ at $P \leq 0.05$.

between crops and perennial weeds in subsequent growing seasons in ways not previously appreciated, as considered below.

Ozone Effects Assessment Protocols

Research on plant responses to O_3 has included various experimental approaches using controlled environment, greenhouse, field chambers and free-air systems (Manning and Krupa 1992; Morgan et al. 2006; US EPA 2006; Flowers et al. 2007). The largest dataset relating O_3 exposures to crop responses was obtained by the US EPA National Crop Loss Assessment Network (NCLAN) program, which used regression modeling approaches based on concentration-response experiments conducted in open-top field chambers (OTC) to estimate ambient O_3 effects on various crop species (Heagle 1989). Ozone effects data on crops were also produced by the European Open-Top Chambers Programme (EOTCP) (Jäger et al. 1992), the European Stress Physiology and Climate Experiment (ESPACE) (Bender et al. 1999), the CHanging climate and potential Impacts on Potato yield and quality program (CHIP) (Vorne et al. 2002), and in a number of similar but unaffiliated studies (US EPA 1996; US EPA 2006). Yield loss functions were developed for many crops, generally in monoculture, in a variety of environments. The data overwhelmingly indicated production losses due to O_3 exposure in the OTCs. However, considerable variability was observed between and within species, between years, irrigation regimes and environments. Nevertheless, OTCs have provided consistent indications of yield losses for a wide variety of plants due to O_3 exposure (Heagle 1989; US EPA 2006). Open-top chambers are suitable for studying the effects of O_3 because plants can be grown in close to natural conditions while O_3 concentrations can be maintained below phytotoxic levels with filtration or increased by additions of O_3. However, plant growth conditions are altered by OTCs. For example, differences in plant growth may be caused by higher air turbulence in the chamber compared with ambient air (AA), which promotes O_3 incursion into the lower canopy. Plants tend to be taller inside OTCs compared with plants grown in AA, probably due to an average 12% decrease in light inside OTCs (Heagle 1989). There is also increased light penetration into the lower portion of the plant canopy, particularly adjacent to chamber walls if border plants are not used, and daytime air temperature inside an OTC averages 2 °C higher than ambient. These changes in environmental conditions inside OTCs, the relatively small plot size and the single factor protocol with O_3 as the only variable have led some to question the extrapolation of OTC data to normal field conditions (for example, Manning and Krupa 1992; Nussbaum and Fuhrer 2000; Morgan et al. 2006).

There is evidence, however, that OTCs do not significantly affect the relative response of plants to O_3 despite modest alterations in microclimate conditions. Combined results from 24 experiments with 11 crop species (alfalfa (*Medicago sativa* L.), clover (*Trifolium repens* L.) – tall fescue (*Festuca arundinacea* L.), cotton (*Gossypium hirsutum* L.), lettuce (*Lactuca sativa* L.), maize (*Zea mays* L.), peanut, sorghum (*Sorghum bicolor* (L.) Moench.), soybean, tobacco and winter wheat) indicated that average yield in OTCs supplied with non-filtered air (NF) was similar to that in AA (5% ± 17% greater in NF than in AA) (Heagle 1989). In a study with snap bean (Burkey et al. 2005), plants were treated with charcoal-filtered air (clean air control, CF) and NF air in OTCs as well as with AA (Table 2). Both NF and AA treatments provided similar O_3 exposures of approximately 40 nL/L with and without potential chamber effects. A comparison of NF/CF and AA/CF ratios clearly showed that O_3 reduced the pod yield of sensitive genotypes in both treatments, while the effect was greater in AA. In a study with peanut, biomass production and yield were not significantly different in NF air and AA treatments, although stomatal conductance was 12% lower in the AA treatments (Booker et al. 2007; Burkey et al. 2007). These differences may reflect minor chamber effects or experimental variability, but do not indicate that OTCs overestimated the actual impact of ambient O_3.

Table 2. Ozone effects on mature pod yield of snap bean grown in Raleigh, North Carolina during the summer of 2003

Genotype	CF pod yield (g/plant)	NF pod yield (g/plant)	AA pod yield (g/plant)	NF/CF	AA/CF
BBL-274 (T)	134 ± 9^{a}	142 ± 5^{a}	110 ± 6^{b}	1.08 ± 0.12	0.83 ± 0.01
BBL-290 (S)	110 ± 10^{a}	$86 \pm 7^{a,b}$	68 ± 8^{b}	0.78 ± 0.06	0.63 ± 0.11
R123 (T)	85 ± 8^{a}	80 ± 4^{a}	70 ± 4^{a}	0.96 ± 0.09	0.85 ± 0.12
R331 (T)	116 ± 9^{a}	108 ± 12^{a}	76 ± 6^{b}	0.94 ± 0.09	0.66 ± 0.09
S156 (S)	100 ± 10^{a}	64 ± 9^{b}	32 ± 6^{c}	0.65 ± 0.07	0.32 ± 0.04

Plants were grown in 15-L pots containing Metro Mix 200 with optimized fertilization and irrigation. Plants were exposed from emergence through mature pod harvest to charcoal-filtered air (CF, 15 nL/L O_3) (seasonal 12-h mean) or non-filtered air (NF, 40 nL/L O_3) in open-top chambers or to ambient air (AA, 41 nL/L O_3) in adjacent plots. Yield was assessed as mature pod dry weight at the end of the growing season. NF/CF and AA/CF ratios were calculated from paired chambers and AA plots using a randomized complete block design. Values are means ± *SE* for three replicate plots per treatment. For each row, yield values followed by a different letter were significantly different ($P < 0.05$). S, sensitive; T, tolerant.

Caution is warranted, however, when extrapolating OTC results to generalized AA conditions. The natural environment and local growth conditions normally differ between locations and may lead to different concentration-response relationships. Thus, large scale experiments such as NCLAN, EOTCP and ESPACE were conducted in a variety of geographic regions. In addition, elevated temperatures in OTCs can accelerate phenological development and shorten the grain-fill period in cereals such as wheat and rice, which may confound estimates of ambient O_3 effects on grain yield.

Fortunately there are viable alternatives to the use of OTCs, and they have produced results mostly consistent with OTC experiments. Alternatives include chamber-less air exclusion systems that reduce O_3 concentrations in field plots (Olszyk et al. 1986), free-air exposure systems such as SoyFACE (Morgan et al. 2006) and mini open-air systems (Erbs and Fangmeier 2005), zonal air pollution systems (ZAPS) (Runeckles et al. 1990), antioxidant or protective chemicals, paired comparisons of closely related genotypes differing in O_3 sensitivity and exploitation of ambient O_3 gradients (Lin et al. 2007; Manning and Krupa 1992). These approaches address limitations of OTCs and other chamber experiments and facilitate exposure of larger biological units, in some cases small areas of intact ecosystems. Yet each technique poses its own set of uncertainties, from experimental artifacts to spatial heterogeneity in soil and atmospheric properties across larger plots. Available evidence suggests that OTCs do not fundamentally alter plant responses to O_3 and that OTCs remain a useful tool for testing species sensitivity and developing O_3-response relationships (US EPA 2006). Soybean responses to O_3 in a free-air exposure system in the Midwestern USA (SoyFACE) indicated yield losses similar to those previously reported using OTCs (Morgan et al. 2006).

Measured air concentrations of O_3 at some height above the surface have been generally used in establishing cause-effect relationships for vegetation. However, the O_3 concentration gradient between the typical O_3 monitoring height (3 m) and the canopy level measured in many experiments needs to be accounted for in quantifying actual exposures (Nussbaum and Fuhrer 2000; US EPA 2006). It is the dose taken up or absorbed by the plant canopy that results in a response. This is a standard postulate of toxicology that must be reintroduced into air quality effects research. The exchange of gases between the atmosphere and the phytosphere is governed by the ambient O_3 concentration, the turbulent conductivity of the lower atmosphere and the sink properties of the plants and soil. The dynamics of ambient O_3 concentrations are inherently coupled to the meteorology that governs its synthesis and its deposition through effects on plant physiology (NARSTO 2000; National Resource Council 1991). Indeed, a flux-based metric may help to reconcile responses observed in different exposure systems (Pleijel et al. 2007; Matyssek et al. 2008).

However, seasonal-average or flux-based approaches do not capture O_3 exposure dynamics on a daily basis and their relationship to growth stages with differing sensitivities. For example, in soybean, elevated O_3 exposure during mid-to-late-growth stages generally caused a greater yield loss than exposure during early growth stages (Heagle et al. 1991). In tomato, the effect of O_3 on ripe fruit number and production was greatest in the early harvest compared with later harvests due to delayed fruit ripening (Calvo et al. 2007). Krupa and Nosal (1989) applied a statistical model with ambient O_3 exposure variables (hourly median, peak values, percentile statistics, etc.) defined for discrete portions (15-d intervals until harvest at 45 d) of alfalfa growth. Although growth between 15 and 30 d (the exponential phase) appeared to be the most sensitive, at each growth stage there was a strong tendency for the hourly median value to be the first in the order of importance, followed by the cumulative integral of exposure concentration and duration (Krupa and Nosal 1989). Overall, similar studies are urgently needed to understand the stochasticity of O_3 exposure and crop response and their corresponding spatial and temporal variability.

Most O_3 studies have been single factor or two-way interaction experiments between O_3 and such factors as NO_2, SO_2, acid deposition, nitrogen availability, water stress and elevated CO_2 (Heagle 1989; US EPA 1996; Fiscus et al. 2002; Fuhrer and Booker 2003). The effects of ambient O_3 in combination with more than two other environmental factors have been little explored. This line of investigation deserves more attention as it has been shown in rice, for example, that the magnitude of the O_3 and elevated CO_2 responses and interactions can be influenced by high temperature episodes, nutritional status and intra-plant competition (Reid and Fiscus 2008). Plant responses to O_3 are highly influenced by site conditions, and comprehensive assessment of their relative influences needs more study, especially in a changing climate. This issue is important to air quality regulators, crop breeders and producers, ecosystem managers and climate modelers.

Ozone Effects on Yield

Ozone sensitive crop and horticultural species include alfalfa, bean, clover and other forages, cotton, grape (*Vitis vinifera* L.), lettuce, oat (*Aveva sativa* L.), peanut, potato (*Solanum tuberosum* L.), rape (*Brassica napus* L.), rice, soybean, spinach (*Spinacia oleracea* L.), tobacco, tomato, watermelon (*Citrullus lanatus* (Thunb.) Matsum and Nakai) and wheat (Heagle 1989; Synder et al. 1991; Krupa et al. 1998; Benton et al. 2000; Morgan et al. 2003; Burkey et al. 2007; Ainsworth 2008; Feng et al. 2008). Combining NCLAN data obtained from 12 species comprising 38 cultivars and applying a Weibull statistical function indicated that cultivars of seven species (cotton, peanut, spinach, soybean, tomato, turnip (*Brassica rapa rapa* L.) and wheat) would exhibit 10% yield losses when exposed to a 7 h seasonal average O_3 concentration ≤ 50 nL/L (AOT40 ≤ 7 μL/L × h) (US EPA 1996). Species such as maize, sorghum, barley (*Hordeum vulgare* L.) and some wheat cultivars required a 7-h seasonal average O_3 concentration > 80 nL/L (AOT40 > 35 μL/L × h) to suffer a 10% yield loss. Meta-analyses of O_3 effects studies on rice, soybean and wheat found that seasonal O_3 concentrations averaging 62, 45 and 42 nL/L lowered yields by 14%, 10% and 18%, respectively, compared with CF air controls (Morgan et al. 2003; Ainsworth 2008; Feng et al. 2008). An extensive survey of season-long field studies conducted in OTCs found that bean, cotton, lettuce, onion (*Allium cepa* L.), soybean, tomato, turnip, watermelon and wheat suffered 5% yield losses at seasonal AOT40 values of 6 μL/L × h or less (O_3-sensitive crops) (Mills et al. 2007). Yields of broccoli (*Brassica oleracae*), grape, maize, potato, rape, rice, sugar beet (*Beta vulgaris* L.) and tobacco were suppressed by 5% at seasonal AOT40s of 8.6 to 20 μL/L × h (moderately O_3-sensitive crops) (Mills et al. 2007). Ornamental plants such as petunia (*Petunia × hybrida*) and buddleia (*Buddleia davidii* Franch.), fruit bushes (blackberry (*Rubus cuneifolius* Pursh)) and landscape shrubs can also be injured by ambient O_3 (Cathey and Heggestad 1982; Findley et al. 1997a, 1997b; Chappelka 2002). Injury can occur as a loss in biomass or yield, foliar necrosis and pigmentation, or a decrease in flowers or species fitness, or alteration in fruit quality. Nutritional quality also declines in some forages (Krupa et al. 2004; Lin et al. 2007).

Agronomic crop yield loss due to ambient O_3 in the USA is estimated to range from 5% to 15% (Heagle 1989), worth \$US3–5 billion annually (Fiscus et al. 2005; US EPA 2006). If anthropogenic O_3 was eliminated in the USA, the increased production value of eight major crops was estimated as \$US2.8 to \$5.8 billion in 1990 (Murphy et al. 1999). This constitutes a relatively minor, but non-trivial, portion of the total cost of air pollution on society (Murphy et al. 1999). However, the database for these estimates is limited. In addition, wide variability in O_3-sensitivity among various crop cultivars is common, with variation in sensitivity within species often as great as differences among species (US EPA 2006).

Genetic Variability in Ozone Sensitivity

Genetic variation within and among species in their O_3 response is commonly observed. One way to obtain insight about the effects of ambient O_3 on plants is to compare the growth and productivity of closely related plant cultivars and clones that differ in injury or growth responses to O_3. This has been done with soybean, wheat, tobacco, clonal clover and selected bean lines (Heagle 1989; Barnes et al. 1990; Heagle and Stefanski 2000; Burkey et al. 2005; Cheng et al. 2006). In experiments using AA exposures in New York, North Carolina and California, ambient O_3 concentrations were sufficient to cause 25%, 39% and >50% biomass reductions, respectively, in the sensitive clone compared with the tolerant clone of white clover (Heagle et al. 1995). Similarly, in North Carolina, yield reduction was observed in sensitive versus tolerant cultivars of snap bean grown in AA (Burkey et al. 2005). Snap bean pod yield declined more than 30% in AA for the O_3-sensitive “Bush Blue Lake 290” (BBL-290) variety, with much smaller losses observed for the O_3-tolerant “Bush Blue Lake 274” (BBL-274) (Table 2). Yield losses exceeded 60% for the O_3-sensitive genotype S156, an experimental snap bean line developed as an O_3 bioindicator (Burkey et al. 2005). Smaller losses were observed for the comparable O_3-tolerant lines R331 and R123. Significantly, the losses observed in this study for sensitive genotypes occurred under conditions where the seasonal 12-h mean ambient O_3 concentration was 41 nL/L, a level comparable to the 40–50 nL/L range commonly observed in many agricultural regions in the USA.

Additionally, in a field study on Long Island, New York, snap bean fresh market pod yield of the sensitive line (S156) was reduced by as much as 56%, and mature bean yield was reduced up to 66% by ambient O_3 compared with the O_3-tolerant line (R331) (Table 3). When O_3 concentrations were relatively low, as during the third, late-season planting in 2006, O_3 injury was less, and yield differences between the sensitive and tolerant lines were lower compared with yield responses at higher O_3 concentrations during earlier plantings (McGrath and Davey 2006). The similar yields at low ambient O_3 concentrations and a significant O_3 concentration-response relationship (Figure 3) demonstrate that these lines may provide a suitable biological tool for assessing the impact of ambient O_3 in the field.

Results obtained with sensitive and tolerant crop lines, as with all experimental systems, have their own limitations. For example, the pairs of O_3-sensitive and tolerant plants can differ in growth rate, size and performance, although the differentially-sensitive snapbean lines S156 and R123 are similar in size and productivity in low-O_3 air under field conditions (Burkey et al. 2005; Flowers et al. 2007). However, in a controlled environment experiment with high relative humidity, optimum temperature and natural light levels, the sensitivity of the O_3-tolerant R331 line to O_3 on a unit exposure basis was not significantly different from the O_3-sensitive S156 line, based on seed dry mass (Flowers et al. 2007). This illustrates how plant responses to O_3 can vary depending on environmental conditions, culture method and the end point used for performance evaluation (fresh market pod mass versus seed dry mass).

One possible way to avoid problems associated with comparing the responses of different genotypes to O_3 is to use only the sensitive line and to treat half of the plants with a compound that protects against O_3. One such compound is the O_3-injury suppressing chemical ethylenediurea (EDU). Generally good results have been obtained using clover, peanut and snap bean as experimental systems (Ensing et al. 1986; Manning and

Table 3. Average yield (± *SE*) of the O_3-tolerant line R331 compared with the sensitive snap bean line S156 when field-grown under ambient O_3 conditions on Long Island, New York

		O_3 exposure		Fresh market yield (g/plant)			Mature bean yield (g/plant)		
Year	Seeding date	M12 (nL/L)	AOT40 (μL/L × h)	R331	S156	*P*-value	R331	S156	*P*-value
2005	17 May	42.6	7.09	123.5 ± 22.0	102.9 ± 17.2 (−17%)	<0.06	11.2 ± 2.7	6.2 ± 1.4 (−45%)	<0.06
	17 June	44.2	9.25	199.8 ± 22.5	101.3 ± 11.7 (−49%)	<0.01	10.5 ± 1.2	6.3 ± 1.4 (−40%)	<0.05
	13 July	45.4	10.00	137.6 ± 7.6	53.3 ± 1.0 (−61%)	<0.001	16.1 ± 0.7	5.5 ± 0.5 (−66%)	<0.001
2006	25 May	49.3	12.08	141.1 ± 13.9	80.2 ± 8.4 (−43%)	<0.02	10.8 ± 1.0	4.9 ± 0.4 (−55%)	<0.01
	3 July	45.5	10.19	139.2 ± 9.1	99.6 ± 7.7 (−28%)	<0.001	11.1 ± 1.3	7.7 ± 0.4 (−31%)	<0.1
	31 July	37.4	4.27	73.8 ± 4.5	69.2 ± 0.7 (−6%)	<0.14	6.1 ± 0.7	5.2 ± 0.6 (−15%)	<0.6
2007	14 May	45.8	7.50	134.9 ± 14.8	103.8 ± 16.4 (−23%)	<0.08	16.6 ± 2.8	10.4 ± 1.9 (−37%)	<0.06
	12 June	46.7	9.68	260.4 ± 9.6	180.4 ± 5.1 (−31%)	<0.01	22.5 ± 0.7	11.6 ± 0.4 (−48%)	<0.001
	11 July	42.7	6.98	139.0 ± 28.9	98.2 ± 16.3 (−29%)	<0.23	14.0 ± 2.0	6.3 ± 1.1 (−55%)	<0.02

Ozone exposure values were determined from plant emergence through 77 d after planting, which was around the time of the last harvest for fresh market yield and expressed as M12 (average O_3 concentration between 08.00–20.00 h EST) and as AOT40 (accumulated O_3 dose over the threshold of 40 nL/L over this time period). Pods at size for fresh market yield were harvested three to six times from four replicate plots of 15 plants each. Mature bean yield was determined by weighing dried seed from additional plots after plant senescence. In the columns labeled S156, values in parentheses are percent difference between R331 and S156 yields. *P* values were determined by means comparison of yield values by planting date for the two bean lines using ANOVA.

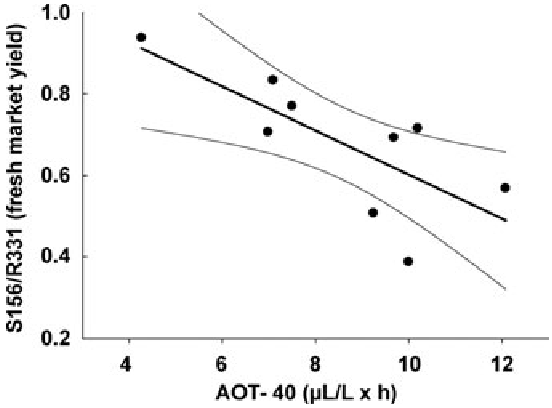

Figure 3. Ratio of S156:R331 fresh market bean yields versus AOT40 (μL/L × h) for O_3-sensitive (S156) and -tolerant (R331) snap bean lines grown in the field in Long Island, New York (Table 3). A linear model is shown ± 95% confidence intervals ($P < 0.02$, adjusted $R^2 = 0.49$).

Krupa 1992; Miller et al. 1994); however, with this technology as with the others mentioned above, uncertainties exist regarding the influence of EDU treatment regimes, interactions with other environmental factors and potential genotype-specific responses to EDU (Miller et al. 1994).

Ozone Effects on Product Quality

In addition to reductions in biomass or crop yield, studies indicate that there are economically important effects of ambient O_3 on the product quality of crops and forage species (US EPA 1996; Black et al. 2000; Ashmore 2005). Visible symptoms on marketable portions of crops and ornamental plants can occur with seasonal 7-h mean O_3 exposures of 40 to 100 nL/L. Spinach with visible injury often is unmarketable; consequently, spinach production has been curtailed where ambient O_3 reaches high levels.

Changes in quality traits have been studied in a limited number of crops (Black et al. 2000; Fuhrer and Booker 2003). In wheat, O_3 increased grain protein concentration but decreased grain and protein yield on an areal basis (Fuhrer et al. 1990; Pleijel et al. 1999; Feng et al. 2008; Piikki et al. 2008). A compilation study of 13 OTC experiments with spring wheat in northern Europe found no statistically significant effect of O_3 on wet and dry gluten values, grain water quotient, starch concentration or Hagberg falling number (an indicator of α-amylase activity in the endosperm) (Piikki et al. 2008). Ozone often shortened the grain-filling period and enhanced maturation and senescence development (Black et al. 2000; Feng et al. 2008; Piikki et al. 2008).

Seeds from soybean exposed to 1.5 × ambient O_3 concentrations showed small changes in oil content, no changes in protein, minor suppression of oleic acid ($C_{18:1}{}^{\Delta 9}$) production and small increases in linoleic acid ($C_{18:2}{}^{\Delta 9,12}$) concentration (Heagle et al. 1998). In peanut, elevated O_3 effects on market grade characteristics were small (Burkey et al. 2007). No treatment effects were observed on the protein and oil contents of seeds, but there were changes in fatty acid composition. Added O_3 increased stearic acid ($C_{18:0}$) and decreased lignoceric acid ($C_{24:0}$) concentrations about 10% compared with the control (Burkey et al. 2007).

A study with potato plants exposed to an AOT40 value of 12.5 μL/L × h in OTCs found that paste from tubers was more viscous (Donnelly et al. 2001). In plants treated with an AOT40 exposure of 27.1 μL/L × h, starch granules were less resistant to swelling, and total glycoalkaloid content was increased. Such increases in glycoalkaloid content have been observed previously in potato (Pell and Pearson 1984) and may be important because glycoalkaloids cause bitter flavors and, at higher concentrations, toxicity. In the CHIP program, the effects of O_3 were studied using OTCs at six sites in northern Europe. Reducing sugar and starch concentrations in tubers decreased linearly due to O_3 exposure, while ascorbic acid concentration increased (Vorne et al. 2002). Compared with the control, exposure to an AOT40 value of 14 μL/L × h decreased starch concentrations by 2%, decreased reducing sugar concentration by 30% and increased ascorbic acid concentration by 20%. Although the changes in reducing sugars and ascorbic acid increased tuber quality, the reduction in starch concentration was considered undesirable.

Ozone added to ambient air was found to reduce yield quality of Eurol rape seed in a free-air exposure system in the UK (Ollerenshaw et al. 1999). Yield quality measured as crude protein (%N × 6.25) and oil content was decreased by 5% to 6% at elevated O_3 (80 nL/L, 6–7 h/d). Short-term pulses of O_3 (66 and 130 nL/L, 8 h/d) during the growth of rape (cv. Licolly) in indoor controlled-environments were found to reduce yield most during flowering and induced changes in seed fatty acid content (Kollner and Krause 2003).

Watermelon foliage often shows injury from ambient O_3. Injury symptoms were first observed in a commercial field in southern Indiana during the early 1980s and consisted of premature chlorotic spots, followed by stippling and bleaching of foliage and necrosis (Decoteau et al. 1986). Mature leaves were more affected than younger leaves. Ozone levels exceeded 50 nL/L daily for 9 h (11.00–20.00 h) in southern Indiana during the growing season. Watermelon (cv. Sugar Baby) grown as an autumn crop in OTCs in Indiana showed a significant decrease in marketable yield by weight and number (21%) for plants grown in NF air compared with those grown in CF air (Synder et al. 1991). In two studies using OTCs in commercial fields in Spain, the soluble solids content of watermelon was decreased 4% to 8% due to ambient O_3 levels (Gimeno et al. 1999).

In grape grown in the northeast US, the variety Chambourcin treated with NF air in OTCs had 18% of their leaves injured, whereas comparable plants in the clean-air treatment had less than 2% foliar injury. In contrast, the variety Vidal, which is considered tolerant to O_3, had less than 6% of its leaves injured in the NF air treatment and less than 1% of its leaves were injured in the clean-air treatment. Berry harvests made in late September and early October suggested that ambient O_3 decreased Vidal grape fruit size, increased juice total acidity in both cultivars, with no effect on juice pH or Brix (total sugars) content (Table 4). In the variety Welschriesling grape, grown in large containers and treated in OTCs with CF air, NF air or added O_3 in a multi-year study, substantial O_3 effects on yield and soluble carbohydrate content of the fruit were observed (Soja et al. 2004). The effects of O_3 on organic acid content were not statistically significant. The study concluded that assessment periods for determining O_3 effects on perennial crops should cover more than one growing season in order to better reflect the biology of many fruit crops because the potential for development of buds into healthy shoots is determined in the previous growing season (Soja et al. 2004).

A study of five tomato cultivars treated in OTCs with CF air, NF air (AOT40–2.5 μL/L × h) or NF air with added O_3 (AOT40–49.9 μL/L × h) in Spain found that sensitivity to O_3 varied among cultivars as indicated by vegetative biomass production, number of ripe and unripe fruit at various harvests and ripening rate (Calvo et al. 2007). There were significant effects of added O_3 on early fruit harvest production, but not at later harvests. Added O_3 reduced total ripe fruit number and delayed ripeness rate, but by the end of the experiment, no significant production decreases due to O_3 were observed because established fruits eventually ripened and mass per fruit increased in one cultivar. Brix degree was lower by 7% to 10% in two sensitive cultivars in the NF treatment and was 10% to 19% lower in four cultivars in the added-O_3 treatment.

Table 4. Effects of charcoal-filtered air (CF, 18 nL/L O_3, seasonal 12-h mean), non-filtered air (NF, 30 nL/L) and ambient air (AA, 33 nL/L) on Chambourcin and Vidal berry mass and juice pH, Brix[1] and total acidity from plants grown in open-top chambers in Biglerville, Pennsylvania in 2004

	Fruit mass (g/100 berries)		pH		Brix (°)		Total acidity	
Treatment	Chambourcin	Vidal	Chambourcin	Vidal	Chambourcin	Vidal	Chambourcin	Vidal
CF air	258 ± 8^a	177 ± 2^a	3.4 ± 0.1^a	3.5 ± 0.1^a	20.7 ± 0.7^a	22.6 ± 0.9^a	8.74 ± 0.26^a	6.94 ± 0.38^a
NF air	236 ± 7^a	172 ± 2^{ab}	3.4 ± 0.0^a	3.5 ± 0.1^a	20.1 ± 0.2^a	22.6 ± 0.5^a	8.78 ± 0.29^a	6.38 ± 0.20^a
AA	233 ± 9^a	161 ± 7^b	3.3 ± 0.1^a	3.4 ± 0.1^a	19.2 ± 0.4^a	21.4 ± 0.3^a	10.40 ± 0.20^b	8.70 ± 0.45^b

Plants were field-established in 2002 with optimized fertilization and irrigation. Treatments began on 1 May and ended after last berry harvest on 4 October. Fruit was harvested on 23 September for Chambourcin and 4 October for Vidal. Values are means ± *SE* for two independent experimental blocks. For each column, values followed by a different letter were significantly different ($P < 0.05$).

[1] Brix is used for measuring the approximate amount of sugars juice. For fruit juices, one degree Brix is about 1%–2% sugar by weight (Pandell 1999).

In the case of perennial grasslands (pastures and rangelands), relevant long-term effects of O_3 may develop over several years. Forage quality can be changed because of O_3 effects on leaf chemistry, which could be a direct effect on secondary metabolism or a change in plant development (Fuhrer and Booker 2003). In a grass-clover forage study conducted in OTCs in Raleigh, North Carolina, for example, white clover leaf *in vitro* dry matter disappearance and nitrogen concentration declined, while neutral detergent fiber increased in AA compared with CF air (Burns et al. 1997). Decreased yield and quality of O_3-exposed bahiagrass (*Paspalum notatum* Fluegge) (Muntifering et al. 2000) and sericea lespedeza (*Lespedeza cuneata* (Dum. Cours.) G. Don) (Powell et al. 2003) were of sufficient magnitude to have nutritional implications in their use by mammalian herbivores (Krupa et al. 2004). Likewise, a decline in relative feed value of high-yielding alfalfa in Alberta, Canada was strongly linked to ambient O_3 concentrations, based on a multivariate analysis of air pollutant and meteorological data (Lin et al. 2007). Interactive effects of O_3 with other air pollutants on plant quality have also been reported. For example, results from a long-term experiment in a Swiss sub-alpine pasture revealed that positive responses in forage quality to nitrogen inputs were negated by increased lignification of cell-wall constituents associated with accelerated foliar senescence due to elevated O_3 (Cline et al. 2008). Similarly, Sanz et al. (2005) reported that nitrogen fertilization amplified O_3 effects on the concentration of the ligno-cellulose fraction in subterranean clover (*T. subterraneum* L.). Decreased nutritive quality of forages can lead to lower milk and meat production from grazing animals, thus linking air quality with impacts on animal production systems (Krupa et al. 2004).

Ozone Interactions with Herbicide Efficacy and Invasive Species

Previous studies have suggested that O_3 can influence the efficacy of some agricultural chemicals, depending on exposure protocols, plant sensitivity to the herbicide and O_3, O_3 concentrations and other environmental factors such as light intensity (Dixon et al. 1996). Herbicides that induce the formation of toxic levels of ROS in plants may be less effective in situations where O_3 has stimulated antioxidant metabolism, which increases their resistance to the herbicide effect (Dixon et al. 1996). For example, in young sugar beet plants exposed to 100 nL/L O_3 7 h/d for 2 d in growth cabinets, followed 3 d later by treatment with phenmedipham at prescribed rates, suppression of shoot fresh mass and chlorophyll concentration in the combined O_3 plus herbicide treatment was less than would be expected if the negative effects of the two treatments were additive (Dixon et al. 1996). Activities of several important antioxidant enzymes were stimulated by both treatments, suggesting that upregulation of antioxidant metabolism by O_3 resulted in plants better adapted to resisting increased ROS stress from certain herbicides. Conversely, a number of fungicides, herbicides and growth regulators can protect plants against O_3 injury (US EPA 1996). Some of the fungicides are carbamates, which are also used as antioxidants in manufactured materials such as rubber products for protection against ambient O_3 and UV radiation damage (US EPA 1996).

Horseweed (*Conyza canadensis* (L.) Cronquist) is native to North America, but is becoming newly invasive. This has coincided with the development of resistance to the widely used herbicide, glyphosate. The glyphosate-resistant (GR) biotype that has emerged in the San Joaquin Valley (SJV) of California is unusual in that it is more robust with greater seedling and rosette development than the sensitive (GS) wild-type progenitor. The SJV biotype of GR exhibits no fitness penalty of herbicide resistance, as is usually observed (Baucom and Mauricio 2004). This advantage in vigor declined with increasing O_3 concentrations (4, 59 and 114 nL/L, 12-h daily average) in plants treated in greenhouse chambers (Grantz et al. 2008). Although early experiments suggest that evolution of resistance to glyphosate is not linked with increased resistance to O_3, there was a biologically significant impact of the combination of O_3 and glyphosate. The additive impact of O_3 and glyphosate was much more devastating to the GS biotype than to the GR biotype, particularly on above-ground productivity. Individuals of the GS biotype were reduced to non-viable leaf area and biomass, and seedling survival in GS was significantly lower than in GR at all O_3 exposures tested (Grantz et al. 2008). In the absence of glyphosate, both biotypes remained viable, even at the highest O_3 concentration. At moderate to high O_3 concentrations the GS biotype was effectively removed from experimental populations in the presence of glyphosate, while the GR biotype remained viable. The combination of O_3 and glyphosate has the potential to accelerate the fixation of the GR allele in unmanaged horseweed populations and thereby contribute to the recent aggressive spread of GR horseweed in California, a previously unrecognized impact of oxidant air pollution on unmanaged plant populations.

Yellow nutsedge is a widespread weed that is difficult to control in many cropping systems in arid regions. It is a C_4 species that reproduces largely vegetatively. Pima cotton (*G. barbadense* L.) is more sensitive to O_3 than is nutsedge in both above and below-ground productivity. Ozone directly suppressed the productivity of cotton and enhanced the competitiveness of nutsedge (Grantz and Shrestha 2006). In contrast, nutsedge was most competitive with tomato at moderate O_3 concentrations (Shrestha and Grantz 2005), though the sensitivity of nutsedge to O_3 restored the competitiveness of tomato with further increases in O_3. In these cases it was possible to predict competitive outcomes qualitatively based on the relative sensitivity of the individual species to O_3. However, in many cases competition is complex and such simple relationships break down (Evans and Ashmore 1992). Overall, inter-specific differences in their sensitivity to O_3 can lead to shifts in competition for space, nutrients and water in mixed populations of crop and weed species, particularly in the case of perennial crops.

Concluding Remarks

In general, it is important to remember that O_3 at sufficiently high concentrations is toxic to most living things. Our present understanding of crop responses to O_3 indicates that measurable yield losses due to O_3 toxicity are likely occurring in food and fiber crops in many regions of the world (Emberson et al. 2001; Mauzerall and Wang 2001; Fuhrer and Booker 2003; Wang and Mauzerall 2004; Ashmore 2005; US EPA 2006). Quality aspects of affected vegetation can be lowered by O_3 as well. Ozone concentrations continue to rise in some regions of the world, but if proposed emission control legislation is implemented worldwide, O_3 concentrations in 2030 are projected to stabilize at 2000 levels except in regions (e.g. India) with large increases in energy, transportation and industrial activities (Dentener et al. 2006). Rising levels of atmospheric CO_2 will likely ameliorate deleterious O_3 effects on vegetation, although the converse is also true – O_3 suppresses the potential CO_2 aerial fertilization effect in some plants as well. Overall, efforts to mitigate climate change are also projected to lower ground-level O_3 concentrations and radiative forcing (West et al. 2007). However, climate models also suggest that episodes of high ground-level O_3 concentrations will occur more frequently during the growing season in regions such as the northeastern USA and Southeast Asia due to increases in temperature and changes in atmospheric circulation patterns (Mickley et al. 2004; Dentener et al. 2006). Damaging effects of ambient O_3 on yield and quality of many crops and horticultural plants will continue in many areas of the world and require further scientific evaluation of magnitude, distribution and mechanism.

Understanding the impact of ambient O_3 under open field conditions is especially relevant to current agricultural practices where new crop cultivars, many of which are genetically modified, are being placed into production without specific consideration of their sensitivity to O_3. Crop breeding programs need to incorporate selection of traits for improved plant tolerance to ambient O_3 in order to maintain and increase crop yields and nutritive quality.

However, a full assessment of ambient O_3 impacts on food crop and ornamental plant performance is likely to be complex. Growers may not be aware of yield losses due to O_3 when sensitive cultivars are no longer grown near resistant ones, when distinctive symptoms do not occur on more resistant cultivars and particularly when yield losses on adapted, O_3-resistant cultivars are not identified because there is no clean-air control for comparison under commercial production conditions. Yield losses due to O_3 exposure have been reported in cases where no visible injury symptoms were observed (Reich 1987; US EPA 1996). Powell et al. (2003) observed altered foliar chemistry and decreased forage nutritive quality in the absence of foliar injury. In contrast, visible foliar injury was observed in five tomato cultivars following O_3 exposure, while a range from little to significant reductions in biomass and yield were found among the plant lines (Calvo et al. 2007). Thus, visible foliar O_3 injury might not always be a reliable indicator of potential O_3 effects on biomass production, yield and product quality. Environmental conditions influence ambient O_3 effects and inter-annual variability in weather conditions makes generalizations difficult. It is challenging to assess yield loss in the field and to diagnose O_3 symptoms without comparisons of biomass and yield responses at a range of O_3 concentrations.

There is currently consensus within the scientific community that O_3 can have significant effects on many crop and horticultural plants (Heagle 1989; Chameides et al. 1994; Emberson et al. 2001; Ashmore 2005; US EPA 2006; Mills et al. 2007). This has been demonstrated through studies using a variety of approaches such as: outdoor controlled-environment chambers, OTCs, free-air exposure systems, open-air experiments with sensitive/tolerant cultivars and O_3-protectants, and multivariate modeling of plant responses to ambient O_3 using multiple study locations and similar experimental protocols. The protocols have been used in various combinations to screen crops and cultivars for O_3 sensitivity. To refine the range of likely losses will require updating and expanding previous studies using modern cultivars grown under current production conditions of fertility and water management. Potential gains achieved by screening modern cultivars for O_3 sensitivity using marker-assisted selection is an unexplored arena. Further studies are needed to: (i) define crop responses to O_3 under a range of environmental conditions; (ii) identify molecular markers for O_3 sensitivity; (iii) assess plant responses to ambient O_3 in natural settings; and (iv) construct predictive models of crop performance in a changing climate. These are costly studies to conduct and have not been carried out for currently-used cultivars.

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