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Exogenous application of chemicals for protecting plants against ambient ozone pollution: What should come next?
Costas J. Saitanis and Evgenios Agathokleous

Abstract
Elevated ground-level ozone (O₃) pollution can adversely affect plants and inhibit plant growth and productivity, threatening food security and ecological health. It is therefore essential to develop measures to protect plants against O₃-induced adverse effects. Here we summarize the current status of phytoprotection against O₃-induced adverse effects and consider recent scientific and engineering advances, to provide a novel perspective for maximizing plant health while reducing environmental/ecological risks in an O₃-polluted world. We suggest that nanoscience and nanotechnology can provide a new dimension in the protection of plants against O₃-induced adverse effects, and recommend that new studies are based upon a green chemistry perspective.

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Introduction
Concentrations of ground-level ozone (O₃) have increased throughout the northern hemisphere since the industrial revolution [1—4]. Urban, suburban, rural, and remote areas are generally exposed to elevated O₃ levels, in terms of both average and maximum concentrations, and mathematical models suggest that this environmental issue may persist over several coming decades [1—4]. Moreover, an analysis of air quality after the lockdown imposed in global cities during the COVID-19 pandemic revealed a considerably amplified O₃ pollution in cities [5], highlighting the complexity of this environmental issue and the difficulty to reduce O₃ pollution [5].

Elevated O₃ concentrations may negatively affect human health [3,6] and are potentially phytotoxic, suggesting a risk for vegetation, ecological health, and environmental sustainability in the long term [3,4,7,8]. Chronic exposure of vegetation to elevated O₃ concentrations can lead to development of visible leaf injury (Fig. 1), decreased productivity of plants, altered interactions between plants and associated insects and microbes, and impaired ecological processes such as nutrient and water cycling and decomposition [7,9]. Biodiversity of terrestrial ecosystems may also be at risk [7], and yields of major crops, such as wheat and rice, may be reduced [10], posing a threat to global food security. For instance, O₃ may inhibit annual forest tree biomass growth by 11—13%, rice yield by 8%, and wheat yield by 6% in China, translating to O₃-induced economic losses of 52.2, 7.5, and 11.1 billion US$, respectively [10]. Hence, biosphere sustainability may be at risk as a result of vegetation exposure to elevated O₃ concentrations, demanding the development of methodologies to protect plants against O₃-induced damage. The need of such plant protection methodologies becomes even more important when considering that the levels of O₃ (a secondary pollutant) can remain potentially phytotoxic even in cases where strict regulations to reduce the emissions of primary pollutants are imposed [5] because of complex reactions in the atmosphere as well as transboundary transportation of O₃ and its precursors.

Developing O₃-tolerant cultivars would be beneficial, but this is a challenging task, especially for trees, whose breeding requires a long time and considerable resources. Ozone-tolerance quantitative trait loci have been identified in crop plants, and associated genes have been identified by profiling assays [11]. Recently, a screening of monosomic lines of ‘Chinese Spring’ wheat for O₃ response revealed that chromosome 7 A was a major contributor to O₃ tolerance (assessed by the extend of foliar injury), making one further step into decrypting crop tolerance genome determinants [12].
of Asian crops can be facilitated by the application of an antiozonant into real-world conditions [13], and the biological results need to be incorporated into breeding programs for developing O₃-tolerant cultivars while maintaining the quality for human feeding. Therefore, the development of O₃-tolerant cultivars is possible, but practically time- and resource-demanding, and, seemingly, difficult to happen in developing countries, suggesting that other methodologies to protect plants against O₃ damage are urgently needed.

Here, we present and discuss current status and recent trends in the field of plant protection against O₃-induced injury, to offer a perspective for environmental safety, ecological health, and food security in an O₃-polluted world.

Nonantiozonant substances: can they enhance the performance of plants against O₃ stress?

Some 70 years have passed since Middleton et al. [14] first reported the results of a trial to evaluate the efficacy of aqueous sprays of manganese, zinc ethylene-bisdithiocarbamate, and bordeaux to protect pinto bean leaves against O₃-induced injury, and numerous chemicals have been tested since then (Fig. 2).

Among the tested chemicals, many pesticides were found to partially protect plants against O₃-induced phytotoxicity (and in some cases with an important degree of protection), although the applied doses have rarely been assessed by proper tests of dose—response relationships covering a reasonable dose—response continuum (Fig. 3) [15,16]. The ‘overall protection’ by fungicides could be due to (i) a reduced fungal activity, (ii) an enhanced plant capacity to cope with O₃-induced stress [15], or both (i) and (ii). Using pesticides for protecting plants against O₃-induced phytotoxicity would be beneficial to reduce the agricultural costs because the same agrochemical would theoretically serve a dual purpose: to inhibit the target pests and enhance plant capacity to cope with O₃-induced stress. However, recent scientific advancements suggest important agricultural risks. In particular, an array of research programs has demonstrated that low doses of stresses stimulate not only plants, but also microorganisms, insects, and other potential agricultural pests [17—19]. This stimulation often has intergenerational and intragenerational effects and acts as a hormetic preconditioning vehicle, which can enhance the tolerance of pests to pesticides and potentially lead to intragenerationally attained resistance [17,19]. Hence, low doses of pesticides that protect plants against O₃-induced phytotoxicity may be that low to finally stimulate pests populations outbreak, leading to pesticides tolerance or resistance in the same or subsequent generations. Therefore, the use of pesticides in the agricultural practice for protecting plants against O₃-
induced phytotoxicity should be re-examined by new generation research programs that consider nontarget effects to various generations of pests.

Micronutrients and plant growth regulators are widely applied in the agricultural practice, and some of them may also protect plants against O₃-induced toxicity [15]. However, only a few projects have evaluated the latter possibility, and, thus, their capacity and mode of action to protect plants against O₃-induced toxicity remains poorly understood. Thus, no general conclusions can be drawn from the available literature.

Several antioxidants have been also tested, but most studies suffer from limitations (e.g. low-resolution dose–response assessment), not permitting any general understanding of their role as potential plant protectants against O₃-induced phytotoxicity [15]. However, a number of studies have shown that exogenous application of the ascorbic acid antioxidant improves the performance of plants under O₃-induced stress, albeit there is no conclusive evidence proving that O₃-tolerance degree is related to endogenous ascorbic acid content [20]. New studies should consider that the location and/or availability of ascorbic acid may be more important to protect plants against O₃-induced stress than its total content [20]. New researches should also direct to examine whether exogenous application of ascorbic acid, as a protectant against O₃-induced stress, affects the plant signaling mechanism [20]. Nearly all the studies testing antioxidants as potential plant protectants against O₃-induced phytotoxicity have been conducted in facilities isolating plants either fully (e.g. closed growth chambers) or at a large degree (e.g. open-top chambers) from the natural environment. Therefore, it remains unclarified whether changes in the signaling mechanism due to ascorbic acid alter the interaction between plants and plant pests under field (real-world) conditions, suggesting potential agricultural and ecological risks. This is a critical issue because stimulation of plant pests may cause considerably larger damage/injuries to plants than the current average ambient O₃ concentrations of the northern hemisphere.

Physical barriers to O₃ entrance into plant tissues, such as antitranspirants and oils, have been also tested. Although they may offer some protection by impeding O₃ via limited uptake and reactions at the leaf surface, their application into the agricultural practice is difficult because they concurrently impede CO₂ uptake, thus, potentially inhibiting plant productivity [15,16,21].

**Antiozonants: the current focus**

Antiozonants are chemical compounds protecting materials, such as plastics and rubber, against O₃-induced damage [22]. The most efficient and almost exclusively used protectant against O₃-induced damage nowadays is ethylenediurea (EDU) [15,23,24]. EDU is a synthetic chemical, which was used as antiozonant in tires and
other materials and found to protect plants against O3-induced damage. Over 50 plant species, of which more than 35 crops and numerous cultivars, were found to be benefitted by the effects of EDU [15,23–30]. A meta-analysis summarizes that EDU increased significantly plant height (8%), stem weight (17%), root biomass (20%), number of leaves (7%), leaf biomass (19%), stem diameter (13%), chlorophylls (7%), carotenoids (13%), and photosynthetic rate (8%) across experiments and taxa [25]. In crops, it significantly enhanced the number of ears, pods, tubers, or fruits per plant (24%); the weight per grain, seed, tuber, or fruit (5.6%); and the number of grains/seeds per ear/pod (7.5%) [25]. Therefore, EDU offers a modest enhancement of the performance of many plant traits under O3-induced stress. However, although EDU appears to protect plants within a hormetic framework (Fig. 3) [31], the underpinning biological mechanisms are not fully understood [15,23,24,31]. Notwithstanding, it was recently shown that EDU can protect plants not only endogenously (systemically after entering plant tissues) but also exogenously by reacting with O3 on the leaf surface [32].

EDU, however, has some important shortcomings. First, it is used at high amounts (e.g. compared to nanomaterials and other agrochemicals), and the implications of its application in the environment are unknown. Second, considering the applying concentrations and the potential accumulation in the agricultural products, the implications to the health of humans and other animals consuming such products are unknown. Third, its complexity as a molecule and the lack of other uses in the agricultural practice make EDU very expensive and available only by few laboratories for research purposes. Because of its limitations, alternatives should be invented to protect plants against O3-induced damage, availing of the most contemporary science, engineering, and technology.

Phenylurea is a component of EDU (the chemical structure can be found in the study Manning et al. [22]), which was also shown, in some studies, to protect plants against O3-induced injury [23,33]. Although studies show that phenylurea is not as effective as EDU, those studies included only doses of phenylurea equal to the applied doses of EDU. However, because phenylurea protects significantly against O3-induced phytotoxicity, it can be hypothesized that it may be a hormetin (such as EDU) [23,31]. Hence, phenylurea should be seen as an independent chemical (rather than an EDU constituent) to study its own biological capacity, that is, to understand whether phenylurea is as effective as EDU in protecting against O3-induced phytotoxicity, assays evaluating the full dose–response continuum are needed, incorporating doses both sub–no-observed-adverse-effect-level (NOAEL) and above-NOAEL (Fig. 3). Potential replacement of EDU by phenylurea would offer an important perspective for further developments because the chemical structure of phenylurea is simpler than that of EDU [22]. Therefore, experiments addressing the effects of phenylurea on plants under O3-induced stress are encouraged.

**Nanomaterials: a contemporary alternative?**

Nanomaterials (chemical substances/materials) are manufactured and used at a tiny scale and came to revolutionize science and technology as well as the agricultural practice [34–38]. Nanomaterials can be used in agriculture to ensure food security and improve environmental quality because of less input and less waste produced than conventional products and approaches [34,35]. Nanoagrochemicals, including nanopesticides, display a 20–30% median gain in efficacy relative to conventional products [38].

After applied to plants, nanoparticles, via the symplastic and apoplastic pathways, reach the xylem and phloem vessels and translocate across tissues and organs [39]. Many kinds of nanomaterials, at low concentrations, were found to protect several plant species and genotypes against negative effects of various stressors. They can prevent programmed cell death, accumulation of reactive oxygen species, accelerated senescence, and inhibition of photosynthesis, growth, vigor, and productivity [40–43], which are key targets of O3 negative effects as well.
An extensive literature analysis shows that nanomaterials stimulate higher plants by ~25% on average, across types of nanomaterials, plant species, and plant traits; the maximum stimulation is commonly <200% [42]. However, the maximum stimulation depends on the nanomaterial applied, application method, growth stage of application, plant trait endpoint, and exposure duration [42]. This analysis revealed many mechanisms of plant response to nanomaterial, which seem capable to counteract ozone-induced damage, all executed within the framework of hormesis [42]. Furthermore, the degree of stimulation by nanomaterials [42] appears to be sufficient to alleviate the damage induced by environmentally realistic O$_3$ levels, which is commonly <30% for wheat and other crops [10,44–46].

These suggest that new research programs may focus on the potential application of nanomaterials as a novel tool for protecting plants against O$_3$-induced phytotoxicity, but the environmental fate and effects on nontarget organisms should be studied too. The current developments in nanoagrochemicals [36–38] can facilitate the development of research programs aiming at protecting plants against O$_3$ negative effects by applying nanomaterials.

**Recommendations**

Considering the substantial lack of evaluations of dose–response relationships with agrochemicals as potential plant protectants against O$_3$ negative effects, newer studies should focus on evaluations of dose–response relationships of agrochemicals, by incorporating several sub-NOAEL doses/concentrations, when comparing agrochemicals.

Transdisciplinary research programs incorporating biology, chemistry, and engineering are needed to potentially lead to breakthroughs in plant protection against O$_3$ negative effects. In particular, focus should be placed on the following tasks:

- Developing slow-release chemicals to potentially reduce the application interval, which commonly ranges between 7 and 15 days [23].
- Reducing the amount of chemicals needed for sufficient protection against O$_3$ damage, while optimizing the degree of protection, by moving from the conventional chemicals to nanochemicals. In doing so, as chemical mixtures induce hormesis as well [47], mixtures including xenobiotics and naturally occurring compounds (e.g. plant growth regulators) could be tested for protecting plants against O$_3$-induced stress while regulating their growth at the most optimum degree. However, the solving principle of *lex parsimoniae* (law of parsimony) suggests that chemical structures and solutions should be kept as simple as possible.
- Developing chemicals or nanomaterials that have a high capacity to protect plants against O$_3$-induced toxicity and degrade faster in the environment would reduce environmental/ecological risks.
- Targeting sustainable chemistry of plant protectants against O$_3$-induced toxicity, and in particular via the building block of green chemistry [48], would help to comply with the goals of the United Nations 2030 Agenda for Sustainable Development.

Recent studies have also attempted to manipulate O$_3$ effects on plants by inoculating symbiotic microorganisms to enhance plant tolerance to O$_3$ [49]. Although this is premature, further researches may provide an opportunity to combine chemical and biological methodologies in the future. The experience from extensive research projects on the role of plant growth—promoting microorganisms in improving plant tolerance to other abiotic factors causing oxidative stress (e.g. drought) [50] can provide an excellent source of knowledge for making a step further.

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