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Perspective

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# Plant biochemistry influences tropospheric ozone formation

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**Abstract**

Tropospheric ozone ($O_3$) is among the most damaging air pollutant to plants. Plants alter the atmospheric $O_3$ concentration in two distinct ways: (i) by the emission of volatile organic compounds (VOCs) that are precursors of $O_3$; and (ii) by dry deposition, which includes diffusion of $O_3$ into vegetation through stomata and destruction by nonstomatal pathways. Isoprene, monoterpenes, and higher terpenoids are emitted by plants in quantities that alter tropospheric $O_3$. Deposition of $O_3$ into vegetation is related to stomatal conductance, leaf structural traits, and the detoxification capacity of the apoplast. The biochemical fate of $O_3$ once it enters leaves and reacts with aqueous surfaces is largely unknown, but new techniques for the tracking and identification of initial products have the potential to open the black box.

**Keywords:** Antioxidant; Biogenic volatile organic compounds; Glandular trichomes; Ozone; Reactive; Oxygen; Species, Stomata

## Introduction

### Tropospheric $O_3$ formation

**$O_3$** in the stratosphere filters UV radiation, but in the **troposphere** $O_3$ is a damaging air pollutant to human and plant health [Environmental Protection Agency EPA. Tropospheric $O_3$ (trioxygen) is an allotrope of oxygen that forms through chemical reactions with two chemically distinct precursors: nitrogen oxides ($NO_x = NO + NO_2$) and reactive carbon molecules including carbon monoxide (CO), methane ($CH_4$), and **VOCs** Rates of $O_3$ formation depend on sunlight and the relative concentrations of $NO_x$ and reactive carbon molecules; namely, methane and VOCs [.]. The reaction of nitric oxide (NO) with the peroxy radical ($R\dot{O}_2$) is the central reaction for the formation of $O_3$ in the troposphere. In this reaction, NO is converted to $NO_2$ which is rapidly photolyzed to form $O_3$ and recycle NO. The efficiency with which $O_3$ is produced from **$NO_x$** pollution varies with the location and time of emissions. For example, in the polluted regions at the Earth's surface, $NO_x$ rapidly reacts to form $HNO_3$, which serves as a reservoir for $NO_x$. In less polluted areas, $NO_2$ photolysis competes more effectively with $HNO_3$ production and more molecules of $NO_x$ react with peroxy radicals to form $O_3$. In regions where $NO_x$ is propelled into the free troposphere, like the tropics, $O_3$ production is especially efficient. Additionally, the VOC:$NO_x$ ratio determines the $O_3$ concentration. In urban areas with elevated $NO_x$ due to high emissions, $O_3$ formation is limited by VOCs, leading to locally suppressed $O_3$ concentrations. $NO_x$ transported away from urban centers can mix with VOCs, resulting in greater $O_3$ concentrations in suburban areas [1].

### VOCs

Plants produce a vast diversity of biogenic VOCs, including isoprene, monoterpenes, and higher terpenoids .Terrestrial vegetation emits isoprene at high levels (~400–600 Tg C year$^{-}$) and isoprene has high chemical reactivity in the troposphere .The tropospheric lifetime of isoprene is only ~ –2 h and it is rapidly oxidized by hydroxyl radicals, $O_3$, and nitrate radicals ($NO_3$). The degradation of VOCs leads to the formation of peroxyl radicals. Those react with NO to form $NO_2$, which then photolyzes to form $O_3$ In areas with very low $NO_x$, peroxy radicals formed from isoprene oxidation react with each other or $O_3$, resulting in net $O_3$ destruction. Globally, modeling studies estimate that forest-emitted isoprene increases the tropospheric $O_3$ concentration by 5–8% .Isoprene oxidation can also produce peroxyacylnitrates (PANs), which can be transported long distances under cool, high-altitude conditions. The long-distance transport of PANs can contribute to $O_3$ formation far from the pollutant source. Thus, globally, biogenic VOCs contribute to $O_3$ formation in the troposphere, although there is significant variation in isoprene emissions among ecosystems and species .For example, broadleaf forests have average isoprene emissions of 2.6 mg m$^{-2}$ h$^{-}$, needle-leaf evergreen trees emit 2.0 mg m$^{-2}$ h$^{-}$, and crops emit very little, only 0.09 mg m$^{-2}$ h$^{-}$. This variation in emission led to concerns that increasing the planting of isoprene-emitting bioenergy species will increase $O_3$ stress, leading to crop yield loss and increased human mortality [2].

### Stomatal control of $O_3$ deposition

Deposition of $O_3$ to terrestrial ecosystems is a significant sink for $O_3$, and understanding variation among ecosystems and species in $O_3$ uptake is needed for accurate prediction of tropospheric $O_3$ concentrations .Dry deposition occurs when atmospheric turbulence transports $O_3$ close to a surface and then $O_3$ moves through a boundary layer around a surface. $O_3$ dry deposition occurs through **stomata** as well as other, non-stomatal pathways including uptake by leaf cuticles, soil, water, snow, and manmade surfaces. A synthesis of observation studies found that stomatal uptake accounts for 45% of $O_3$ deposition on average across ecosystems. This percentage varies with season and ecosystem, but given a prominent role of stomata in $O_3$ deposition, understanding $O_3$ flux through stomata is a major research focus. To estimate $O_3$ diffusion through stomata, the resistance of stomata to water vapor is multiplied by the ratio of the diffusivity of water vapor to that of $O_3$ (.6 ), with the assumption that the water leaving a leaf is proportional to the $O_3$ entering and that $O_3$ reactions in the leaf do not limit stomatal uptake. Both of these assumptions, that water

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loss is proportional to $O_3$ uptake and that there is negligible resistance to $O_3$ destruction inside the leaf, have been questioned and remain active research areas. Furthermore, long-term exposure to elevated $O_3$ pollution often reduces plant biomass and stomatal conductance, which limits subsequent $O_3$ deposition and can feed forward to increase atmospheric $O_3$ concentration [3].

### The rapid response of stomata to $O_3$

Greater stomatal conductance tends to lead to more sensitivity to $O_3$, often attributable to greater $O_3$ uptake and subsequent oxidative damage. In the model species arabidopsis, natural variation in $O_3$ sensitivity, measured as ion leakage, was correlated with whole-rosette conductance. Additionally, the greater $O_3$ sensitivity of the Cape Verde island accession has been linked to constitutively high stomatal conductance caused by impaired function of mitogen-activated protein kinase [4]. Thus, stomatal closure is a direct way to reduce $O_3$ uptake by leaves and alleviate oxidative damage. Stomatal pores close rapidly in response to acute $O_3$ exposure, followed by reopening, which depends on the $O_3$ treatment concentration and duration . Some low-level $O_3$ exposure may also allow a faster response to higher doses of $O_3$ and therefore provide protection against greater $O_3$-induced injury, a process known as priming. In an experiment with common bean, exposure of leaves to 30 min of 200-ppb $O_3$ before a greater, 600-ppb treatment resulted in greater stomatal closure and lower VOC emissions compared with the 600-ppb treatment alone. The correlation of sensitivity to $O_3$ stress with stomatal conductance, and the fact that stomata close in response to $O_3$, suggest that greater $O_3$ tolerance could be engineered by altering stomatal conductance. Stomata are the entry points for the $CO_2$ used for photosynthesis and so reducing stomatal conductance might also reduce $CO_2$ entry into the leaf and compromise productivity. However, recent work has demonstrated that genetic manipulations to reduce stomatal density only moderately reduced stomatal conductance and did not change photosynthesis, suggesting that there is room to optimize stomatal density to atmospheric conditions [5].

## Conclusion

Identifying the extent to which plant biochemistry and physiology contribute to tropospheric $O_3$ formation, destruction, and deposition will help in understanding the mechanisms that underpin plant $O_3$ sensitivity and improve predictions of global tropospheric $O_3$ concentration. Plant species release more than 30 000 different biogenic VOCs, including reactive classes of non-methane biogenic VOCs such as isoprene, which are emitted in large enough quantities to impact tropospheric $O_3$ concentrations. While isoprene can increase $O_3$ concentrations locally, monoterpenes and higher terpenoid compounds also rapidly react with $O_3$ in the leaf boundary layer and can protect plants from oxidative stress. Deposition of $O_3$ into vegetation is related to stomatal conductance and leaf structural traits. While there is evidence that antioxidants quench ROS within leaves, variation in detoxification capacity among different species is significant and the biochemical fate of $O_3$ once it enters leaves and reacts with aqueous surfaces remains largely unknown New techniques for the tracking and identification of initial products have the potential to shed light on that question and could improve the identification of targets to increase $O_3$ tolerance.

### Acknowledgement

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### Conflict of Interest

None

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