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Emerging challenges of ozone impacts on asian plants: actions are needed to protect ecosystem health

Zhaozhong Feng^a, Evgenios Agathokleous^a, Xu Yue^b, Elina Oksanen^c, Elena Paoletti^d, Hiroyuki Sase^e, Anthony Gandin^f, Takayoshi Koike^g, Vicent Calatayud^h, Xiangyang Yuanⁱ, Xuejun Liu^j, Alessandra De Marco^k, Yves Jolivet^f, Sari Kontunen-Soppela^c, Yasutomo Hoshika^d, Hikaru Sajil^l, Pin Liⁱ, Zhengzhen Li^l, Makoto Watanabe^m and Kazuhiko Kobayashi^{i,n}

^aKey Laboratory of Agrometeorology of Jiangsu Province, School of Applied Meteorology, Nanjing University of Information Science & Technology, Nanjing, China; ^bSchool of Environmental Science and Engineering, Nanjing University of Information Science & Technology, Nanjing, China; ^cDepartment of Environmental and Biological Sciences, University of Eastern Finland, Joensuu, Finland; ^dInstitute of Research on Terrestrial Ecosystems, National Research Council, Sesto Fiorentino, Italy; ^eEcological Impact Research Department, Asia Center for Air Pollution Research (ACAP), Niigata, Nishi-ku, Japan; ^fAgroParisTech, INRA, UMR Silva, Université De Lorraine, Nancy, France; ^gDepartment of Forest Science, Hokkaido University, Sapporo, Japan; ^hFundación CEAM, Valencia, Paterna, Spain; ⁱState Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing, China; ^jCollege of Resources and Environmental Sciences, Key Laboratory of Plant-Soil Interactions of MOE, Beijing Key Laboratory of Cropland Pollution Control and Remediation, China Agricultural University, Beijing, China; ^kDepartment for Sustainability (SSPT), Italian National Agency for New Technologies, Energy and Sustainable Economic Development (ENEA), Rome, Italy; ^lCenter for Environmental Biology and Ecosystem Studies, National Institute for Environmental Studies, Ibaraki, Tsukuba, Japan; ^mInstitute of Agriculture, Tokyo University of Agriculture and Technology, Tokyo, Fuchu, Japan; ⁿGraduate School of Agricultural and Life Sciences, the University of Tokyo, Tokyo, Bunkyo-ku, Japan

ABSTRACT

Context: Ozone concentrations near the land surface are rising in Asia while they are declining or stagnating in Europe and North America. Ozone is the most widespread air pollutant negatively affecting vegetation, and its increased concentrations pose a major threat to food quality and production and other ecosystem services in Asia.

Method: In this review, we provide an overview of scientific challenges in the impacts of ozone pollution on Asian vegetation, and synthesize the challenges toward mitigation of the impacts.

Result: We argue that new policy initiatives need to seek both reduction of ozone levels and enhancement of plant tolerance to ozone to maintain food quality and ensure food supplies.

Conclusion: The scientific advancements must be transferred to actions by two types of institutions: a) environmental agencies for reducing ozone levels and b) agricultural research institutions for enhancing plant tolerance to ozone. In connecting the scientific advancements with the institutional actions, scientists in Asian countries should play the key role taking advantages of interdisciplinary and international collaborations.

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Introduction

Surface ozone (O₃) level is rising over East (Ma et al. 2016), South (Lal et al. 2012), and Southeast (Assareh et al. 2016) Asia, following the rapid economic growth and urbanization. Ozone is a secondary pollutant formed in the atmosphere by sunlight-driven chemical reactions between the precursor gases including nitrogen oxides (NO_x) and non-methane volatile organic compounds (NMVOCs) (The Royal Society 2008). As of 2014, Asia is the world's largest emitter of the two precursors: China emits 30% of NO_x and 19% of NMVOCs, followed by India's emissions of 13% (NO_x) and 11% (NMVOCs) of the global emissions (Hoesly et al. 2018) (Figure 1). Across 30 years from 1980, major contributors to global tropospheric O₃ have shifted from the developed countries in mid- and high-latitudes of the northern hemisphere to the

developing countries in lower latitudes of South, Southeast, and East Asia (Zhang et al. 2016).

Ozone is the most widespread air pollutant threatening agricultural production, biodiversity, and ecosystem services more than any other air pollutant at large spatial scales from national and regional to the entire globe (Tang et al. 2013; Anav et al. 2016; Mills et al. 2018b; Agathokleous et al. 2020; Sicard et al. 2020; Xu 2021). It is also the second most important air pollutant negatively affecting human health after particulate matter (Brauer et al. 2016; Zhang, Wei, and Fang 2019; Orru et al. 2019). The extent of the negative impacts on major crops at current O₃ levels is estimated to be comparable to other major stressors including pests and diseases in many major agricultural areas, including East and South Asia (Mills et al. 2018b). In addition to O₃, Asian vegetation is subjected to atmospheric aerosols (Yue et al. 2017) and acid rain/

CONTACT Zhaozhong Feng  zhaozhong.feng@nuist.edu.cn  Key Laboratory of Agrometeorology of Jiangsu Province, School of Applied Meteorology, Nanjing University of Information Science & Technology, Nanjing 210044, China

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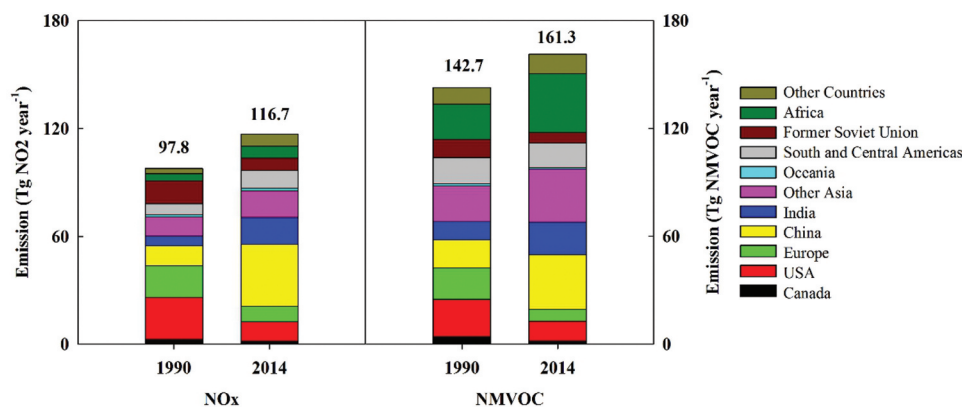


Figure 1. Regional contributions to anthropogenic emissions of nitrogen oxides (NO_x) and non-methane volatile organic compounds (NMVOCs) as of 1990 and 2014. Data were extracted from Hoesly et al. (2018). NO_x emissions are expressed on NO₂ basis. NMVOCs do not include biogenic VOCs (BVOCs).

nitrogen deposition (Liu et al. 2013; Sase 2017). The increasing impacts of O₃ along with the other air pollutants could threaten food security and thereby human nutrition for the still increasing population in Asia, where 60% of the global population resides and major fractions of world's main crop yield are produced, e.g., 90.3% of rice, 43.8% of wheat, and 31.5% of maize (FAOSTAT: <http://www.fao.org/faostat/en/#data> (last access 21 May 2020); based on the period 2014–2018). Considering that ecosystem can be defined as “a dynamic complex of plant, animal, and microorganism communities and the nonliving environment interacting as a functional unit” with humans being an integral part of it (Millennium Ecosystem Assessment 2003), the preceding discussion suggests that O₃ pollution can impact ecosystem health.

Against the challenges of increasing air pollution impacts on vegetation in Asia, concerned scientists have gathered at the Asian Air Pollution Workshop (www.aapw.net.cn) annually from 2015 to 2019. Participants from diverse disciplines including air chemistry, ecology, plant physiology, and soil science shared findings, exchanged opinions, and discussed future collaborations for mitigating the negative impacts of air pollution. Throughout the discussions, the participants have identified current status and future challenges of scientific research in air pollution impacts on vegetation in Asia. Hence, a need has emerged to synthesize the result of this scientific activity with the aim to present the O₃ impacts within the socio-environmental context of Asia, and to set out the roles of scientists in reducing O₃ damages to Asian vegetation.

In this article, we give an overview of progresses and challenges in the science of O₃ pollution impacts in Asia from three aspects: 1. Monitoring, modeling and assessment, 2. Effects of O₃ on plant metabolism and how this threatens food quality and quantity for human and animal consumptions, and 3. Plant contribution to O₃ pollution. We then synthesize the

challenges toward mitigation of the O₃ impacts in Asia. While the article concerns Asia, the discussion is based on available scientific studies, and not all Asian countries have any or sufficient studies on O₃ pollution impacts. Therefore, the article is focused on countries for which there is sufficient available scientific information, e.g., China, India, and Japan. Furthermore, the article is not directed to discuss technical information covered in existing publications (Yamaguchi et al. 2011; Koike et al. 2013; Oksanen et al. 2013; Izuta 2017; Mukherjee et al. 2021; Xu 2021). It is directed to provide to policymakers, scientists working in different research areas, and other stakeholders an integrated synthesis of the issue in Asia, so to translate scientific knowledge into practical actions aiming at protecting the health of both natural ecosystems and managed agroecosystems.

Monitoring, modeling and assessment of ozone impacts in Asia

Monitoring of ozone pollution

International monitoring networks of air pollution in Asia are young and less developed compared to those in the U.S. and Europe. In East Asia, the Acid Deposition Monitoring Network (EANET: <http://www.eanet.asia>) started regular measurements of air pollution and ecological impacts in 2001. As of 2018, O₃ was measured at 25 sites in seven countries. In South Asia, the “Malé Declaration on Control and Prevention of Air Pollution and its likely Transboundary Effects for South Asia” was initiated in 1998, and the monitoring network was established in 2003 (<http://www.rrcap.ait.asia/male>). A total of 15 sites from 8 countries are operated for monitoring O₃ and other pollutants.

National networks have also been built and operated in some countries. For example, the TOAR (Tropospheric O₃ Assessment Report) database accommodates O₃ monitoring data at 1260 sites in Japan, 312

sites in South Korea, but only 26 in China (Schultz et al. 2017). For South Asia, 8 datasets were aggregated in the TOAR database. With these existing data, however, spatial coverage is clearly insufficient in Asia, as shown by the wide gaps of monthly mean O₃ concentrations over Asia on the 5° × 5° grids (Fig. 6 of Schultz et al. (2017)).

However, the situation for China has been drastically improved since 2013, when the Ministry of Environmental Protection of China started publicizing hourly data of major air pollutants including O₃ at 1497 monitoring stations (Li et al. 2018a). In India, a project-based monitoring network for O₃ was started with a few sites in 2008, and the site number grew to 14 in 2015 (Lal et al. 2017). However, a nation-wide monitoring network of air pollution (<https://app.cpcbcr.com/ccr/#/caaqm-dashboard-all/caaqm-landing>) has been developed in India since 2017.

Although these networks serve as foundations for regional air pollution assessment, the lack of uniform criteria and the limitation in spatio-temporal coverage reduce the effectiveness of using their data. Most monitoring stations are located in urban areas, while the stations covering rural and remote forested areas are limited. In addition, most of these networks are not integrated, and associated variables (e.g., meteorology, chemistry, and vegetation) are not often observed simultaneously.

Modeling of ozone pollution and its impacts

Models are useful tools to interpret monitoring data and perform large-scale assessment. However, because of the simplifications and assumptions in the process of modeling, model outputs are confronted with uncertainties from parameterizations, physical processes, and boundary conditions. In air quality modeling, large uncertainties exist due to the discrepancies between the models in model parameters, physical processes, and emission inventories.

Models of O₃ impacts depend on empirical approaches, which characterize the O₃ level as various dose metrics (Agathokleous, Kitao, and Kinose 2018). Some metrics are weighed means or sums of concentrations across a specified period, while others measure the amount of O₃ absorbed by plants (Lefohn et al. 2018). The dose is then used as an indicator of the risks to vegetation (Tang et al. 2014; Mills et al. 2018a; Li et al. 2018a) or converted to damages (e.g., loss of crop yield or lower biomass production) using dose-response relationships (Feng et al. 2012, 2019a). The dose-response relationships have been derived from experiments conducted under manipulated O₃ concentrations in facilities mimicking the real-world environment (Feng, Tang, and Kobayashi 2017). It was found, however, that the dose-response relationships differ between different types of facilities (Feng

et al. 2018c; Agathokleous et al. 2019a). Uncertainties may thus arise from the dose metrics and dose-response relationships (Agathokleous et al. 2019b).

Recently, semi-mechanistic schemes and process-based analyses are emerging for impact modeling (Tian et al. 2016; Yue et al. 2017). Crop yield losses are modeled with explicit description of growth processes in response to O₃ and other environmental changes (Tao et al. 2017; Emberson et al. 2018). Despite these progresses, uncertainties abound in the modeling of pollution impacts due to the diversity of model structures and processes included.

Assessment of risks and impacts due to ozone pollution

Studies conducted in Asia have shown significant crop losses due to O₃ at the present levels (Ghude et al. 2014; Lal et al. 2017; Lin et al. 2018; Feng et al. 2019a). In India, national harvest losses were estimated at 5% for wheat and 2% for rice in one study (Ghude et al. 2014), whereas, in another study, they were in the ranges from 4.2% to 15% for wheat and from 0.3% to 6.3% for rice (Lal et al. 2017). Tang et al. (2013) also estimated the national harvest loss of wheat due to O₃ in the range from 8% to 22% for India, while from 6% to 15% for China. A study on national harvest losses in China estimated the ranges from 21% to 39% for wheat and from 7% to 15% for rice (Lin et al. 2018). More recently, a meta-analytic assessment suggested that Indian major crops rank wheat > mustard > rice > maize in terms of yield sensitivity to ambient O₃, whereas yield sensitivity to elevated O₃ varied with factors such as intrinsic defense response, exposure/dose, and stomatal flux (Mukherjee et al. 2021). Uncertainties thus abound in the estimated O₃ impacts. The harvest losses showed wide ranges even within the individual studies (Tang et al. 2013; Lal et al. 2017; Lin et al. 2018) due to the difference between the dose-response relationships. Some of the relationships were derived from experiments conducted in the same region, whereas others were introduced from Europe or the US. In addition, differences between the air pollution models and emission inventories should have contributed to the large difference between the studies. Even with the same air pollution model, an overestimation of the impact was found when the model outputs were used without the correction for the steep decline in O₃ level near the plant canopy top (Tang et al. 2013).

The uncertainties as noted above have significant implications to the estimates of O₃-induced economic losses in agriculture. Some studies converted the mass-based yield losses to economic losses with the fixed market price and harvested area (Feng et al. 2019a), whereas other studies (e.g., Yi et al. (2018)) used the yield losses as an input to an economic model allowing

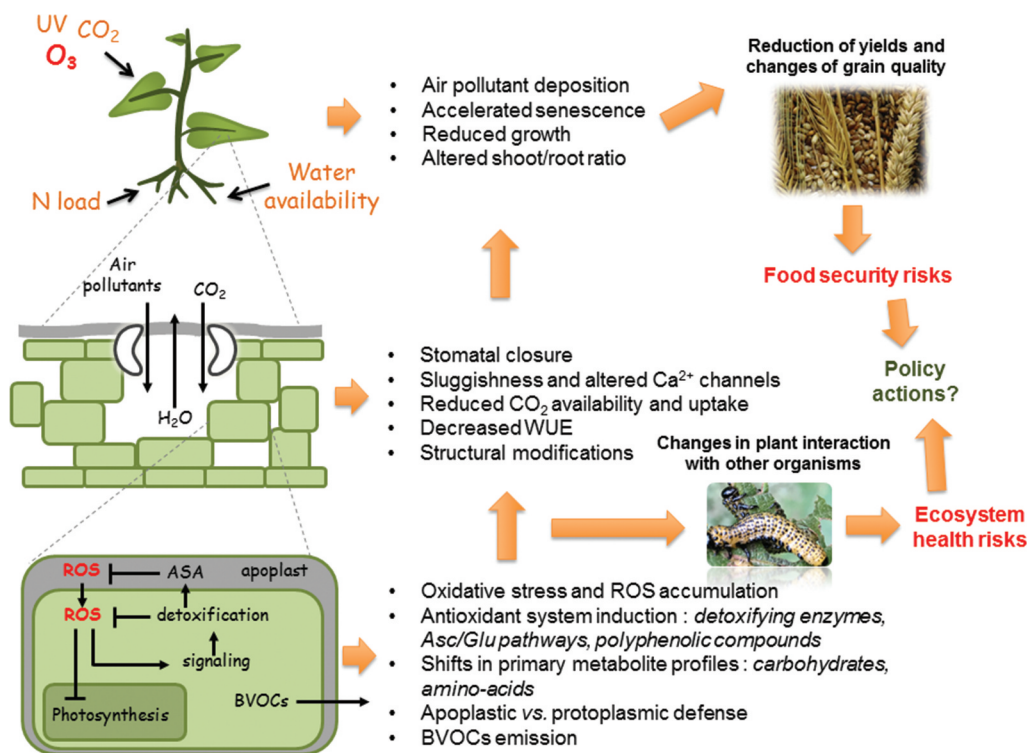


Figure 2. Plant responses to ozone at various scales. ASA: reduced ascorbate; Asc/Glu: ascorbate/glutathione cycle; PS: photosynthesis; Metab. I_r and I_{II}: primary and secondary metabolites; ROS: reactive oxygen species, e.g., H₂O₂, OH.

other variables, e.g., market price, to vary. In either way of estimation, the uncertainties in the yield loss estimate will lead to uncertainties in the economic loss estimate.

In addition to the impacts on quantity of harvested crops, O₃ changes their quality. Protein concentration, for example, is commonly increased by O₃ across species (Wang and Frei 2011), whereas the amount of protein harvested in wheat is reduced because the crop harvest is reduced to a greater extent than the increase of protein concentration (Broberg et al. 2015). It would therefore be misleading to interpret the higher protein concentration in crops grown in elevated O₃ level as an improvement in human nutrition. It is noteworthy that O₃ reduces digestibility of forage crops and crop residues for ruminant animals (Wang and Frei 2011).

Recently, a new regional high-resolution chemical transport model was run over Asia to determine the potential O₃ risk to forests in Asia (De Marco et al. 2020). The authors estimated different concentration-based and dose-based O₃ metrics, which showed different spatial distribution and exceedance extent. A high potential of O₃ impacts on deciduous forest growth in Asia was found, while potential O₃ impacts on evergreen forest types were lower. Most of evergreen forests (86–97%) were potentially exposed to O₃ concentrations exceeding the limits for forest protection, while the percentage of evergreen forests exposed to O₃ doses above the critical levels was lower (12–46%). This study suggests that Asian studies

should focus on dose-based O₃ metrics to provide relevant bases for developing proper standards.

Challenges for monitoring, modeling and assessment

Monitoring data from the existing networks need to be synthesized, while monitoring must be expanded to under-investigated areas, e.g., South Asia. The ground-based monitoring networks could be combined with model simulations to enhance spatial and temporal coverage. The monitoring data shall be valuable in validating the air pollution models, which would be used to estimate surface O₃ over Asia to provide high-resolution inputs for the impact assessments. Application of ensemble predictions with multiple models and emission inventories shall be useful in reducing uncertainties in the prediction of O₃ pollution.

The impact models need to be developed for Asian genotypes, as demonstrated by the greater susceptibility to O₃ in Asian crop varieties than North American (Emberson et al. 2009) and European (Feng et al. 2012) counterparts. The progresses toward the process-based approaches will facilitate the impact models to account for the effects of other interacting variables, e.g., CO₂ concentration and soil moisture. The model uncertainties could be reduced by verifications with observations in the field, for which O₃-FACE (free-air

concentration elevation of O₃) shall be valuable (Oue et al. 2011; Kitao et al. 2015).

Effects of ozone on plant metabolism

Most O₃ impact studies with Asian plants have focused on growth responses, stomatal regulation, and photosynthesis (Izuta 2017), while there is a growing number of studies on biochemical, metabolomic, proteomic or transcriptomic responses (Tsukahara et al. 2015; Zhang et al. 2017). Plants respond to O₃ by adjusting the production of primary metabolites (mainly sugars, organic acids, amino acids) directly involved in growth and developmental processes. In addition, secondary metabolites (a vast group of different organic compounds such as phenolics) are mediating plant acclimation to stressful conditions (Figure 2). Several of these primary and secondary metabolites are essential components of the plant defense systems. If changes in the biosynthetic pathways of such metabolites are likely, omic studies would greatly help to reveal the cellular and molecular mechanisms for plant responses to environmental stresses.

Variation in ozone susceptibility/tolerance between crop species and varieties

A wide variation in O₃ susceptibility/tolerance has been recorded both among and within crop species in Asia. Most studies have been conducted with one or a few varieties, highlighting the requirement for a large-scale screening for genetic variability (Oksanen et al. 2013) as is the recent case of a screening of 40 Indian cultivars of *Amaranthus hypochondriacus* for O₃ tolerance/susceptibility (Yadav, Mina, and Bhatia 2020). For example, large genetic variability in O₃ susceptibility has been found among 18 cultivars of rice and 11 cultivars of wheat in India

(Pandey et al. 2015, 2019), and among 15 cultivars of wheat and 19 cultivars of soybean in China (Jiang et al. 2018; Feng et al. 2018b). In all studies, the genetic variability in O₃ susceptibility was associated with activities in antioxidant systems, especially those involving superoxide dismutase, catalase, glutathione and ascorbate. The antioxidant systems could therefore be a target of interest for engineering O₃-tolerant crops, e.g., rice (Frei 2015).

Antioxidant systems have been well listed but are yet to be better understood regarding the high complexity in their spatial, temporal, and chemical processes (Wang et al. 2015). With this aim, the contributions of the defense systems in the cytosol and cell wall to O₃ tolerance in Asian species have been of particular interest (Feng et al. 2010), but still remain unclear (Wang et al. 2015; Dai et al. 2020). Some research groups working on defense metabolism under O₃ stress attempted to improve current knowledge about the genetic and molecular basis of ascorbate-glutathione pathways (Zhang et al. 2017), the different enzymatic isoforms involved and their respective compartments (Rahantaniaina et al. 2017), other antioxidants within secondary metabolism, such as phenolics (Li et al. 2021), or specific defense structures, such as glandular trichomes (Li et al. 2018b). However, these efforts are still at the initial stages and, thus, the understandings are yet to be developed.

Metabolism in tree species under O₃-induced stress

Asian trees have gained less attention in molecular and metabolite researches compared with the crop species. In Japan, Japanese beech (*Fagus crenata*) has been most intensively studied regarding the metabolism under O₃ pollution (Yamaguchi et al. 2011; Koike et al. 2013). A meta-analysis revealed that temperate

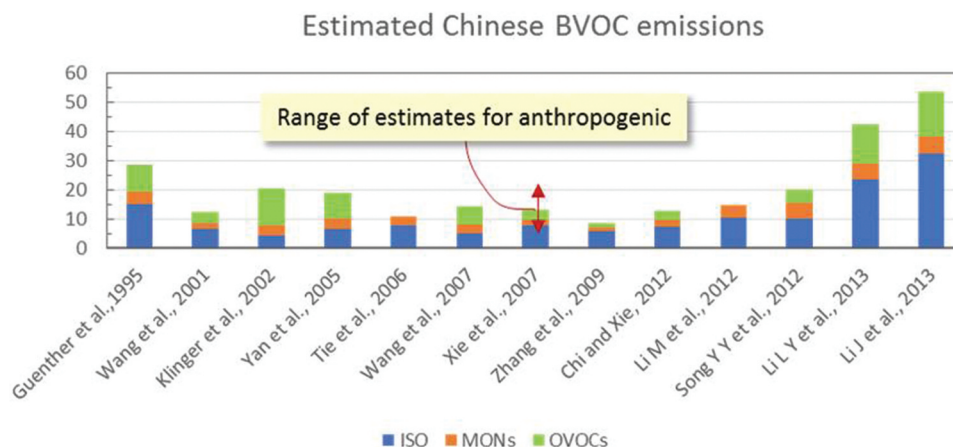


Figure 3. Emissions of biogenic volatile organic compounds (BVOCs) in China at national level as estimated by various studies. ISO: isoprene, MONs: monoterpenes, OVOCs: other BVOCs. Anthropogenic emissions of non-methane VOCs (NMVOCs) are also shown by the range of estimates for years from 2004 onward. References are arranged in chronological order of publication from the left to the right. MONs and OVOCs are combined in the reference 10. See Table S1 for details.

woody species from China were more sensitive to O₃ than those from North America and Europe in terms of gas exchange (Li et al. 2017). Evergreen species are generally more tolerant to O₃ than deciduous species (Li et al. 2017; Feng et al. 2018a; Novriyanti et al. 2021), which can be attributed to the higher leaf mass per area (LMA) in evergreen species (Li et al. 2016; Feng et al. 2018a). Higher LMA is associated with higher tolerance to oxidative stress (Bussotti 2008).

Threats to food quality and quantity for humans and other animals arising from O₃ effects on plant metabolism

As a result of the negative effects of chronic O₃ pollution on plant metabolism, productivity and yields can be highly decreased, including in Asia (see Assessment of risks and impacts due to ozone pollution). These suggest that food quantities in Asia may be threatened by O₃ pollution. However, not only food quantity but also food quality may be threatened by O₃ pollution. That O₃ pollution can affect plant metabolism and biochemistry can be critical when it comes to the quality of food for human and other animal consumption. Imbalance in plant stoichiometry and potential reduction of the overall mineral concentration due to air pollution may affect the quality of human diet (Loladze 2002, 2014). Studies conducted in Japan, using insects as animal models, showed that the behavior and physiology of larvae and beetles of different insect species can be affected when fed with leaves affected by environmental stresses, such as O₃ (Agathokleous et al. 2017, 2019c; Abu Elela, Agathokleous, and Koike 2018). These findings are also supported by studies conducted in other parts of the world showing effects of O₃-stressed plant tissues to animal consumers (see Blande (2021) and Masui et al. (2021) for additional mechanisms driving plant-insect interactions). For example, decreased digestibility was found in rabbits (*Oryctolagus cuniculus*) fed with forage (a mixture of grassland species common in Southern Piedmont, USA) exposed to O₃ concentrations twice the ambient (Gilliland et al. 2012). These suggest a potential threat to the quality of the diet of animals whose nutrition depends upon plants grown in O₃-polluted areas.

Challenges for investigating plant metabolism under elevated O₃

Novel technologies in genomics, proteomics and metabolomics must be fully used in Asia to reveal the molecular mechanisms of tolerance against O₃. Study of defensive metabolites should be related to plant hormones and cell signaling, and extended to special structures, e.g., glandular trichomes, that are active in storing and secreting various secondary metabolites

related to defense against adverse environment (Li et al. 2018b; Oksanen 2018; Karabourniotis et al. 2019). The detoxification capacity could also be related to the internal anatomical mechanism such as high LMA. The quantitative and qualitative understandings of the tolerance mechanisms must be integrated into the models of O₃ pollution impacts.

Plant contribution to ozone pollution in Asia

Plants are not only affected by O₃ but contribute to O₃ pollution by emitting biogenic volatile organic compounds (BVOCs): isoprene, monoterpenes, and other VOCs.

Vegetation as a source of BVOCs

BVOCs play a key role in the formation of O₃. This is because their reactivity is much higher than the anthropogenic NMVOCs (Atkinson and Arey 2003), and their estimated annual emission rate of 80 Tg y⁻¹ (Fu et al. 2007) in Asia is as large as that of anthropogenic NMVOCs from Asia (78 Tg y⁻¹ in Figure 1). Nevertheless, the estimate of BVOC emissions in Asia has large uncertainties. For example, a comparison between the estimates for BVOC emissions from the whole China in the studies after 2000 exhibits a sixfold difference between the lowest and highest estimates (Figure 3).

Among the many factors contributing to this uncertainty, a major contributor is the limited standardization of the emission rate in Asian native species. Many studies have been conducted on BVOCs emission rates in numerous species in China, Japan, and South Korea. For example, data collection from 411 species in China revealed that 88.9% of the studies species emit isoprene, 11.1% emit monoterpenes, and 6.6% emit both (Feng, unpublished data). Generally, broad-leaved species display high isoprene emission rates, especially *Populus* (most common poplar in China: *P. euramericana* cv. '74/76'), *Platanus occidentalis*, *Robinia pseudoacacia*, and *Salix badylonica*, while coniferous species emit high rates of monoterpenes, such as *Platycladus orientalis*, *Pinus griffithii*, and *Pinus armandii* (Jing et al. 2020; Xu et al. 2020). However, these studies often lack uniform criteria and information needed for standardizing the emission rates, limiting a complete understanding of the BVOCs roles in local air quality (Wei et al. 2007) and modeling at continental and global scales (Sindelarova et al. 2014).

Contribution of BVOCs emissions to ozone levels

Contribution of BVOCs emissions to O₃ levels is less studied in Asia than in Europe and North America (Duan et al. 2020). In China, the increase in O₃ concentration by BVOCs is generally five ppb or less in Pearl River Delta (Wei et al. 2007) and the whole eastern

China (Han, Ueda, and Matsuda 2005; Wang et al. 2008), whereas in Yangtze River Delta region, the contribution could be more than 10 ppb or even reach 18 ppb (Liu et al. 2018). High BVOCs-induced O₃ increases were estimated also for the Beijing-Tianjin-Hebei and Sichuan Basin regions, with increases of up to 24 ppb due to the sensitivity of VOC-limited urban areas (Wu et al. 2020). In Japan, an increase of up to 6 ppb was found in monthly mean O₃ concentrations due to BVOCs emissions indicating the strong influences of forest vegetation on O₃ generation (Bao et al. 2010); however, the contributions of BVOCs remain uncertain in other Asian countries.

Responses of BVOCs emissions to rising ozone levels

Emissions of BVOCs could respond to environmental changes (biotic and abiotic), including O₃ (Peñuelas and Staudt 2010; Heil 2014). In Asia, only a few studies have been conducted, and reported inconsistent results. Chronic exposure to higher O₃ increased isoprene and monoterpene emissions in *Ginkgo biloba* trees (Li et al. 2009) and *Pinus tabulaeformis* (Xu et al. 2012), while it reduced isoprene emission from two *Quercus* species (Tani et al. 2017) and two hybrid poplars (Yuan et al. 2017). Monoterpenes emissions from hybrid larch were not affected by O₃ (Mochizuki et al. 2017). A summary of 34 studies conducted in Europe and the US also showed conflicting responses of BVOCs emissions to higher O₃ (Peñuelas and Staudt 2010). There were, nevertheless, more studies reporting significant decreases in isoprene emission than increases, and more studies reporting significant increases in monoterpenes emissions than decreases. Similarly, a recent meta-analysis indicated that isoprene is more sensitive to O₃ and other environmental factors (e.g., elevated CO₂ or drought) than monoterpenes (Feng et al. 2019b).

Challenges for investigating plant contribution to ozone pollution

Quantification of standard emission factors from native and introduced plant species in Asia must be expanded to reduce the uncertainties in the estimates of BVOCs emissions in Asia and to allow an optimal choice of low O₃-forming-potential species for urban greening. The responses of BVOCs emissions to O₃ and other environmental changes warrant further studies to unravel how BVOCs emissions will respond to the changing earth system. Field observations and model estimations should be combined to improve the BVOCs estimates and provide scientific guidance for O₃ pollution control.

Toward mitigation of ozone impacts on plants and ecosystems in Asia

An ultimate goal of air pollution research is to reduce the negative impacts of air pollution. To this end, two approaches are available: (i) to lower the O₃ levels and (ii) to lower the susceptibility of target vegetation to O₃. We argue that, in Asia, both approaches must be pursued in a coordinated effort of policymakers and scientists.

Lowering ozone levels

Lowering O₃ concentration by emission control can provide protection from the O₃ pollution impacts to all the organisms in the target regions. A good example is the success of air quality management in Europe under the framework of the 1979 Convention of Long-range Transboundary Air Pollution (CLRTAP). Under CLRTAP, NO_x emission in Europe was roughly halved since 1990, and sulfur emission was reduced by about 80% in the same period (Maas and Grennfelt 2016).

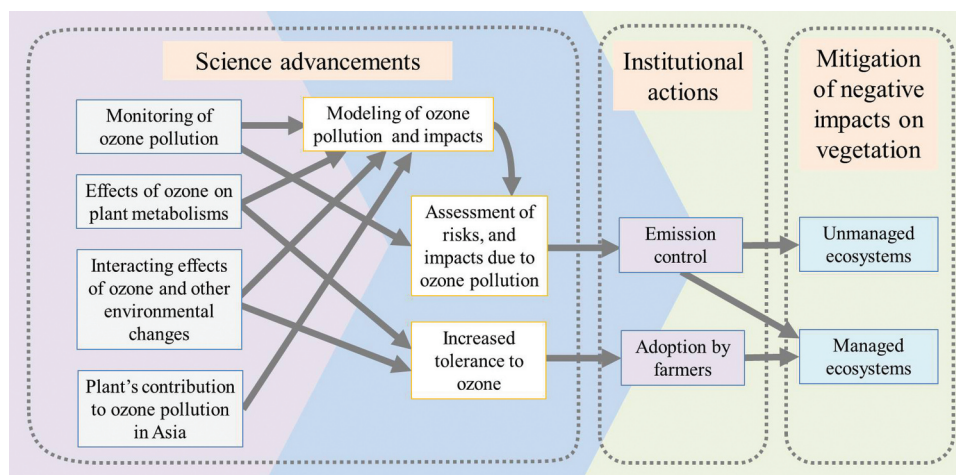


Figure 4. Structure of challenges in order to reduce ozone impacts on vegetation in Asia.

In Asia, however, the emission control shall be more challenging than that in Europe. The major source of the O₃ precursor NO_x is energy production, which will increase with the economic growth in Asia. China is the good example, and India is following suit (Figure 1). Other populous countries, e.g., Indonesia, Pakistan, Bangladesh, Vietnam, are also on track of the economic growth. In 2010, China started to implement the clean air policies, and it is estimated that the emissions have been reduced by 35% for PM_{2.5} and 17% for NO_x through to 2017 (Zheng et al. 2018). This cut in primary pollutant emission clearly is an encouraging development for human health, although there are still nationwide long-term challenges to attain air quality standards (Wang 2021). For protection of vegetation, it could also be good news but to a less extent, since emissions of the other precursor: NMVOC, have increased by 11% for the same period. Therefore, the trends in surface O₃ level and its impacts on vegetation are yet to be investigated.

Against the increasing risk of O₃ pollution on vegetation in Asia, we need to seek other approaches as well.

Lowering the susceptibility of vegetation to ozone

Ozone affects plants after being absorbed via stomata in the leaves (Figure 2). It is therefore possible to lower the O₃ impacts by reducing the gas uptake. Indeed, the faster leaf gas exchange and thereby O₃ uptake has been assumed to be the main cause of higher susceptibility in modern soybean varieties to O₃ than the older varieties (Osborne et al. 2016). It follows that lower gas exchange rate could be a desirable trait for crop varieties under high levels of O₃, as argued for maize under water constraint, where lower-transpiration trait would benefit the crop yield (Messina et al. 2015).

Ozone uptake could also be reduced by partial stomatal closure induced by reduced irrigation, which could also save irrigation water. In rice-growing countries, alternate wetting and drying irrigation has become popular in an attempt to reduce water usage (Carrizo, Lundy, and Linqvist 2017), but it would reduce the O₃ pollution impacts as an unintended benefit (Mills et al. 2018b). Antitranspirants could also alleviate O₃ impacts and water use via reduced gas exchange (Agathokleous et al. 2016). The high O₃ peaks at a sensitive timing of the plant biological life cycle can be avoided by shifting cropping calendar. Such an avoidance measure may be effective in some combinations of location and crop species, if not at global scale (Teixeira et al. 2011).

Besides the reduced uptake of O₃, the impact can also be alleviated by increasing plant tolerance. As mentioned in a preceding section, the genetic variability in O₃ susceptibility relates to activities in antioxidant systems, which could be a good target for

engineering O₃-tolerant varieties. It has been estimated that, by choosing least O₃-sensitive varieties in wheat, soybean and maize, production of the crops could be improved by 12% on global aggregate (Avnery, Mauzerall, and Fiore 2013). They also acknowledged that O₃ impacts could be further reduced by extensive screening and targeted breeding for higher tolerance in the crop species.

The O₃ susceptibility can also be lowered by chemicals, of which ethylenediurea (EDU) has been studied most extensively with a wide range of Asian species and genotypes (Oksanen et al. 2013; Agathokleous et al. 2015; Singh et al. 2015; Jiang et al. 2018; Pandey et al. 2019; Gupta et al. 2020). Understanding mechanisms of the chemical protectants could facilitate development of commercial products for protection of agricultural crops from O₃. The chemical protectants will also facilitate the varietal screening for higher tolerance to O₃ under agronomically realistic environment (Jiang et al. 2018; Pandey et al. 2019; Gupta et al. 2020).

Integrating the approaches for mitigation of ozone impacts

The emission control must not be compromised because of the prospects for higher plant tolerance to O₃, since lowering the O₃ level is the only measure to protect vegetation in unmanaged ecosystems (Figure 4). To this end, monitoring is the critical first step, and the recent development of the nation-wide network of about 1500 monitoring sites has enabled the identification of significant O₃ risks to temperate forests in China (Li et al. 2018a). China's monitoring network will play a critical role in evaluating the efficacy of its efforts for emission control (Zheng et al. 2018).

South Asia is one of the world's hotspots of O₃ pollution impacts (Mills et al. 2018b), but continued monitoring of O₃ concentrations has been limited. A monitoring network equivalent to that in China throughout South Asia would convincingly demonstrate the risks of O₃ pollution, which will motivate the efforts toward the region-wide emission control.

To better support the efforts for emission control, we need progress with improved models to assess O₃ impact on vegetation (Figure 4). The air pollution models will benefit from better developed monitoring networks and understandings of the contributions of vegetation to O₃ pollution. The impact models based on improved understandings of the mechanisms of damages would also have to account for the interaction with other environmental changes (Figure 4).

Recognizing the escalating impacts of surface O₃ and great challenges of emission control in Asia, we need to pursue the measures for increasing plant tolerance to O₃. They are limited to vegetation in managed ecosystems (Figure 4), which, however, does not

downplay their importance. As of 2015, the fractional employment in agriculture is more than 40% in countries of South Asia and 20% in China (ILOSTAT: http://www.ilo.org/ilostat/faces/oracle/webcenter/porta_lapp/pagehierarchy/Page3.jspx?MBI_ID=33 (last update on 9 July 2018)), whereas the fraction is only about 2% in Northern and Western Europe or even less in North America. Negative effects of O₃ pollution on agriculture will directly hit a majority of society members across Asia. In addition, South Asia is among the two regions in the world, along with Sub-Saharan Africa, where food shortage will persist in 2050 (Alexandratos and Bruinsma 2012).

The societal significance of agriculture in Asia shall justify the efforts for developing cost-effective protectants and tolerant varieties. The benefits of this approach could be large. A recent analysis of experimental results from around the world indicated that wheat yield is increased by about 10% by reducing O₃ from the current ambient level (about 40 ppb day-time mean concentrations) to that of pre-industrial times (about 15 ppb) (Pleijel et al. 2018). Such a large reduction of O₃ levels is beyond the feasibility of emission controls, but the genetic or chemical measures could take advantage of the yield increase with the higher O₃ tolerance. Besides the scientific challenges, however, these efforts would face an additional challenge: they have to be adopted by the huge number of farmers (Figure 4). Convincing farmers of O₃ impacts is far from an easy task (Frei 2015), but co-benefits from water-saving and tolerance against other stressors shall facilitate the adoption by farmers. The co-benefits are substantial due to the co-occurrence of O₃ impacts with those by other stressors estimated for South and East Asia (Mills et al. 2018b).

Evidently, scientific findings in the two approaches to reduction of O₃ impacts must be directed to very different audiences: governmental agencies in charge of environmental protection on the one hand, and agronomic institutions from national to local scales on the other hand. The huge diversity of plant production systems in Asia presents intimidating challenges against those who take the latter approach. They can, however, work with scientists in other disciplines, e.g., plant pathology and stress physiology, working for plant protection. In plant breeding also, stress tolerance is among the critical target traits. The real challenge for the latter approach would therefore be to develop interdisciplinary collaborations of scientists toward the common goal: higher food security and better agricultural performances.

Conclusions

We argue that we need both mitigation of and adaptation to the O₃ pollution in Asia. To mitigate emission of O₃ precursors, we need to develop better monitoring

networks and improve the models of O₃ pollution and its impacts. The impact assessment shall benefit from the improved understanding of the plant responses to O₃ impacts and how plants interact with other organisms, such as pests and symbionts. Better understandings of the plant responses shall also help the efforts to increase tolerance in plants against O₃ as adaptation to its risen levels.

To attain the goal of reducing O₃ pollution impacts on vegetation and maintain food security, the scientific advancements need to be transferred to institutional actions: improved emission control by regulatory authorities and adoption of measures for higher tolerance in plants by farmers. To these ends, there must be a community of scientists concerned about the O₃ impacts in each country, where these scientists would play the key role in connecting the scientific advancements with the institutional actions on the international and interdisciplinary collaborations.

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Author contributions

ZF and KK designed the structure. XYue, HSas, XL and ADM authored a first draft of Monitoring, modeling and assessment of ozone impacts in Asia; EO, AG, YJ, SKS and HSaj authored a first draft of Effects of ozone on plant metabolism; EP, XYuan, YH authored a first draft of Plant contribution to ozone pollution in Asia; EA, MW and KK authored a first draft of Toward mitigation of ozone impacts on plants and ecosystems in Asia. XYuan and KK authored a first draft of Table

S1. ZF, EA and KK edited the first draft of the manuscript. All authors revised the manuscript for important intellectual content and approved the final version for submission.

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