Plants and related carbon cycling under elevated ground-level ozone: A mini review

Yanli Zhang [a,b,j,*], Zhiyu Han [a], Xinyi Li [a,j], Hongliang Zhang [c], Xiangyang Yuan [d], Zhaozhong Feng [e], Peng Wang [f], Zhaobin Mu [a], Wei Song [a], Donald R. Blake [g], Qi Ying [h], Christian George [i], Guoying Sheng [a], Ping'an Peng [a], Xinming Wang [a,b,j,**]

[a] State Key Laboratory of Organic Geochemistry and Guangdong Key Laboratory of Environmental Protection and Resources Utilization, Guangzhou Institute of Geochemistry, Chinese Academy of Sciences, Guangzhou, 510640, China
[b] CAS Center for Excellence in Regional Atmospheric Environment, Institute of Urban Environment, Chinese Academy of Sciences, Xiamen, 361021, China
[c] Department of Environmental Science and Engineering, Fudan University, Shanghai, 200438, China
[d] State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing, 100085, China
[e] Key Laboratory of Agrometeorology of Jiangsu Province, Institute of Ecology, School of Applied Meteorology, Nanjing University of Information Science and Technology, Nanjing, 210044, China
[f] Department of Atmospheric and Oceanic Sciences & Institute of Atmospheric Sciences, Fudan University, Shanghai, 200438, China
[g] Department of Chemistry, University of California, Irvine, CA, 92697, USA
[h] Zachry Department of Civil and Environmental Engineering, Texas A&M University, College Station, TX, 77843-3136, United States
[i] Institut de Recherches sur la Catalyse et l'Environnement de Lyon (IRCELYON), CNRS, UMR5256, Villeurbanne F-69626, France
[j] University of Chinese Academy of Sciences, Beijing, 100049, China

ARTICLE INFO

ABSTRACT

Plants play a crucial role in global carbon biogeochemical cycling and natural terrestrial carbon sinks. Dynamic changes in plant-related carbon cycling processes under changing climate and atmospheric compositions are hot scientific issues concerning carbon neutrality. Ozone, as a damaging oxidant, shows a rising trend near the ground where plants grow, directly and indirectly impacting forests and other types of vegetation. This review focuses on the effects of elevated atmospheric ozone levels on plant-related carbon cycling processes, including carbon dioxide (CO_2) assimilation, carbon allocation to roots, volatile emissions, soil carbon sequestration and litter decomposition. Based on previous studies, we propose that field observations, especially *in situ* long-term observations under natural growing conditions in well-designed networks with a better representation, are needed to deeply understand the effects of elevated ozone on plants. Apart from an overwhelming concern about the influence of ozone on crop yields, studies on the effects of elevated ozone on forests, especially tropical and subtropical forests, should be strengthened in the future. Meanwhile, the interactions between ozone and plants should be considered in understanding plants' feedback to oxidants through emissions of volatiles and other trace gases. Moreover, geochemical techniques such as carbon isotopes and molecular markers, along with big data and artificial intelligence approaches, can be extensively used to decode and constrain the ozone-plant relationships, such as those between net primary productivity and ozone.

1. Introduction

As the nexus of carbon biogeochemical cycling in terrestrial ecosystems, plants play a vital role in the global carbon cycle. Green plants can absorb atmospheric carbon dioxide (CO_2) through photosynthesis and therefore forests act as a large and persistent natural carbon sinks (Pan et al., 2011). Plants are also the primary way CO_2 is transferred to soil through roots and litter (Felzer et al., 2005; Sitch et al., 2007;

Ainsworth et al., 2012). Meanwhile, carbon backflows from vegetated lands to the atmosphere through the release of volatile organics from leaves (Guenther et al., 1993, 2012) and the release of CO_2 from the decomposition of soil organic matter and litter (Krishna and Mohan, 2017; Chen and Chen, 2018). Since climate and environmental conditions impact heavily on the physiology of plants, there is a growing concern about the disturbance of carbon cycling, crop yields, and biodiversity by global warming and changing atmospheric compositions (Ainsworth et al., 2008; Bonan, 2008; Wilkinson et al., 2012; Agathokleous and Saitanis, 2020a; Feng et al., 2015, 2019, 2021, 2022; Chaudhry and Sidhu, 2022). Apart from elevated levels of CO_2, atmospheric oxidation capacity is also an emerging factor that significantly influences plants and related issues, such as forest net primary productivity (NPP) and carbon storage (King et al., 2005; Ren et al., 2011; Ainsworth et al., 2012; Chapin and Eviner, 2014; Fuhrer et al., 2016; Yue et al., 2017; Lefohn et al., 2018; Xia et al., 2021).

Ozone (O_3) and its two photodissociation products, hydroxyl radical (OH) and hydrogen peroxide (H_2O_2), are the principal oxidants in the lower atmosphere (Finlayson-Pitts and Pitts, 2000). In recent centuries, especially since the 1950s, vast amounts of ozone-precursor trace gases (e.g., nitrogen oxides, nonmethane hydrocarbons, methane and carbon monoxide) have been released into the atmosphere from human activities (McDuffie et al., 2020), resulting in elevated levels of ambient ozone on global or regional scales (Mills et al., 2018). Ground-level ozone is produced mainly from the complex photochemical reactions of volatile organic compounds (VOCs) and nitrogen oxides (NOx) in the presence of solar irradiation (NRC, 1991; Finlayson-Pitts et al., 1993). As a major component of photochemical smog, ozone has become an air pollution problem in succession from developed to developing worlds (Monks et al., 2015; Schultz et al., 2017; Archibald et al., 2020; Gao et al., 2020). Ozone is also an important greenhouse gas contributing to radiative forcing (IPCC, 2013). There is accumulating evidence that ozone increases significantly not only in populated areas (Lu et al., 2018; Mills et al., 2018; Li et al., 2019; Gao et al., 2020; Sicard, 2021; Wang et al., 2021) but also in background regions with relatively high vegetation coverage (Akimoto, 2003; Cooper et al., 2014; Wang et al., 2017, 2019; Xu et al., 2020; Sicard, 2021). Tropospheric ozone concentrations increased at a rate of 1–5 ppb per decade by the end of the 20th century and are predicted to exceed 80 ppb by the end of this century (Thompson, 1992; Vingarzan, 2004; Sitch et al., 2007; Verstraeten et al., 2015), doubling its current concentrations of 30–40 ppb (Fleming et al., 2018).

As ozone is a strong atmospheric oxidant, elevated ground-level ozone would harm plant growth and human health (Ainsworth, 2017; Wang et al., 2007; Lefohn et al., 2018; Liu et al., 2018; Pleijel et al., 2018; Feng et al., 2022). Extensive studies are available about the impacts of ozone on plant physiology and crop yields (Ashmore, 2005; Häikiö et al., 2007; Velikova et al., 2005b; Agathokleous et al., 2015; Yuan et al., 2017b; Ainsworth et al., 2019), but few focus on plants and carbon cycling with increasing ozone levels. In this review, we put our focus on the influence of increasing atmospheric ozone on plant-related carbon geochemical cycling processes, including assimilation of atmospheric CO_2 by plant leaves, emissions of volatiles from plant leaves, carbon transfer to root and soil, soil microbial activity and decomposition of organics, as well as the decay of litter (Fig. 1).

2. Elevated ozone and CO_2 assimilation

The capacity of the terrestrial biosphere to sequester carbon is governed by the ability of vegetation to capture CO_2 (Oliver et al., 2018). Plants respond to elevated ozone by various physiological mechanisms, ultimately reducing carbon assimilation and changing carbon allocation (Felzer et al., 2007). The injuries to plants caused by elevated ozone can be visible and physiological. Visible injury generally refers to changes in pigmentation or bronzing, fleck, stippling chlorosis, and premature senescence after ozone exposure (Felzer et al., 2007; BroschÉ et al., 2010). The physiological effects of ozone exposure mainly include reducing photosynthesis and gross primary productivity (Ashmore, 2005; Yue et al., 2017), damaging chloroplast and cell membranes (Kangasjarvi et al., 2005; Velikova et al., 2005a), increasing dark respiration (Velikova et al., 2005b), changing carbon allocation, and lowering carbon transport to roots (Qiu et al., 2021) (Table 1).

The uptake of ozone by vegetation is attributed to both non-stomatal and stomatal deposition (Fares et al., 2008). Ozone deposition to
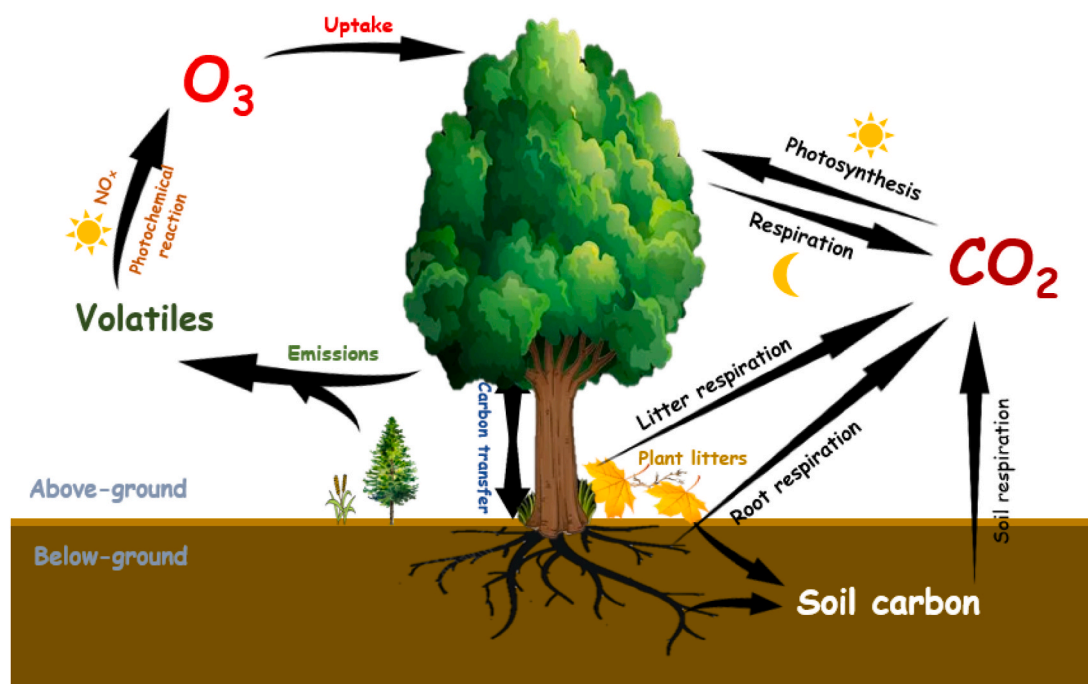

Fig. 1. A conceptual picture effects of elevated atmospheric ozone levels on plants related carbon cycling processes, including CO_2 assimilation, carbon allocation to roots, volatile emissions, soil carbon and litter decomposition.

Table 1
Summary of the injuries to plants caused by elevated ozone.

Variable	Injured	References
Net photosynthesis	–	Ashmore (2005)
Dark respiration	+	Velikova et al. (2005b)
Chloroplast	–	Kangasjarvi et al. (2005)
Cell membrane	–	Velikova et al. (2005a)
Visible	–	BroschÉ et al. (2010)
Crop yield	–	Ainsworth (2017)
Gross primary productivity	–	Yue et al. (2017)
Stomatal conductance	–	Clifton et al. (2020)
Root carbon allocation	–	Qiu et al. (2021)

Note, "**–**" represents negative effects, "**+**" represents positive effects.

vegetation is largely dominated by leaf stomatal uptake during the growing season, while non-stomatal deposition, including deposition to stems, cuticles, soil and other external surfaces, may be larger than stomatal uptake at other times of the year depending on vegetation type and weather conditions (Wittig et al., 2007; Fares et al., 2008; BroschÉ et al., 2010; Feng et al., 2012; Hoshika et al., 2012; Silva and Heald, 2018). Ozone injury in plants depends on the amount of ozone taken up into cells, which is governed by stomatal conductance and plant capacity to detoxify oxygen radicals (Clifton et al., 2020). Ozone can alter stomatal function and cause stomatal closure, leading to changes in assimilation and water use efficiency (Andersen, 2003; Ainsworth, 2017). With the decrease in stomatal conductance to reduce further ozone uptake and damage, CO_2 fixation capacity declines accordingly (Ye et al., 2021).

Once passing the stomata, ozone as a strong oxidant reacts with the apoplast fluid, resulting in the generation of reactive oxygen species (ROS), such as hydrogen peroxide (H_2O_2), hydroxyl radicals (OH·) and superoxide radicals (·O_2-) (Kangasjarvi et al., 2005; Fares et al., 2013). These breakdown products of ozone damage cellular membranes and impair the main metabolic functions (Clifton et al., 2020). Lipid peroxidation and plasmalemma damage in mesophyll cells increase repair costs and initiate a sequence of events leading to chloroplast damage (Andersen, 2003; Grantz et al., 2006; Li et al., 2016). Plant tissues contain enzymes and low molecular mass antioxidants that act as essential components of the cell redox balance and signaling modulation, and play a crucial role in keeping ROS levels under control, reconstituting structures temporarily damaged by acute ozone exposure (Vitale et al., 2007). Reduced ascorbate (AsA) in the apoplast can defend against oxidative pressure due to ozone, acting directly as an electron donor or indirectly in cooperation with the enzymes and metabolites involved in the Halliwell Asada cycle in ROS scavenging (Pellegrini et al., 2018). The antioxidant response is not only limited to AsA, since the detoxification process is a complex network of several types of enzymes, such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD) and metabolites such as polyphenols, carotenoids and proline (Hasanuzzaman et al., 2020). Biochemical repair induces a decline in the activity and concentration of photosynthetic enzymes, and consequently a reduction in CO_2 fixation (Agathokleous et al., 2016; Chaudhry and Sidhu, 2022).

It is worth noting that plants vary in their sensitivity to ozone damage, and the injury of plants is associated with their characteristic ozone tolerance (Velikova et al., 2005b). The main indicators of the ozone susceptibility of plants are stomatal conductance, specific leaf area, and genetically controlled defensive capacity (Tani et al., 2017). Differences in ozone sensitivity among species, genotypes or landraces may be related to plant stomatal control and detoxifying capacity. Ozone-tolerant plants have a stronger ability to control stomata and detoxify ozone and quench ROS than ozone-sensitive plants (Hartikainen et al., 2009; BroschÉ et al., 2010; Yuan et al., 2017a). Typical effects of ozone on sensitive species include alterations of carbon allocation patterns, symptoms of visible injury, enhanced senescence, reduced growth and yield, or reduced flowering and seed production (Bergmann

et al., 2017). For ozone-tolerant plants, elevated ozone may have no significant effects on CO_2 fixation and stomatal conductance (Kivimäenpää et al., 2013). Nevertheless, classifying a species as either ozone sensitive or tolerant might be an oversimplification because the ozone response of a particular genotype seems to reflect its ozone exposure history rather than a generic species-specific trait (Agathokleous and Saitanis, 2020a; Agathokleous et al., 2015). Due to a broad intraspecific variation of ozone sensitivity of plant species, it is a fuzzy and even incorrect terminology to classify the susceptibility of plants to ozone depending on changes in a certain genotype (Monk and Murray, 1995; Oksanen 2003; Ryan et al., 2009; Li et al., 2016, 2017).

3. Elevated ozone and volatile emissions

Trees emit a large quantity and variety of terpenoids, including isoprene, monoterpenes, and sesquiterpenes (Peñuelas and Llusià, 2001; Laothawornkitkul et al., 2009; Pellegrini et al., 2018). Typically, broad-leaved forests mainly emit isoprene, while coniferous forests mainly emit monoterpenes (Guenther et al., 1993). These compounds play important roles in atmospheric chemistry and in plant biology and ecology (Laothawornkitkul et al., 2009). However, increased ozone affects the global carbon cycle by modifying terpenoid emissions (Fares et al., 2013). Terpenoid emissions represent a vital carbon loss to plants' net primary productivity, which is significant for the missing carbon sink or the unknown removal of CO_2 in the atmosphere (Peñuelas and Llusià, 2003; Ryan et al., 2014). As an example, on a global scale, approximately 500 Tg yr^{-1} of isoprene is released from trees into the atmosphere (Guenther et al., 2012). The emitted terpenoids are well known to participate in ozone formation (Chameides et al., 1988, 1992; Calfapietra et al., 2013; Wang et al., 2022), and elevated ozone in turn adversely affects terpenoid emissions. The effects of ozone on plant emissions of terpenoids have been studied in both the laboratory and field using controlled greenhouses or growth chambers, open-top chambers (OTCs), or free-air concentration elevation (FACE) (Hendrey and Kimball, 1994; Calfapietra et al., 2008; Matyssek et al., 2010; Xu et al., 2012, 2015; Yuan et al., 2017a; Feng et al., 2018a). However, this feedback effect of elevated tropospheric ozone on the emission of terpenoids is still a debatable and controversial issue (Calfapietra et al., 2008; Peñuelas and Staudt, 2010; Feng et al., 2018b, 2020) due to the complex direct and indirect effects induced by elevated ozone (Loreto et al., 2004; Calfapietra et al., 2008; Li et al., 2009; Hartikainen et al., 2009; Xu et al., 2015; Ghimire et al., 2017; Mochizuki et al., 2017; Yang et al., 2021).

Terpenoids are antioxidants that protect plants against oxidative stress (Graβmann, 2005; Fares et al., 2008). Although the role of isoprene in plants is not fully understood, there is evidence that it might have a protective role against different oxidative stresses originating from heat shock and/or exposure to ozone (Calfapietra et al., 2008). Endogenous isoprene has been identified as an antioxidant protecting against ozone even at low concentrations (Loreto and Velikova, 2001). Monoterpenes are also found to act as antioxidant compounds to protect plant leaves against ozone and ROS (Ghimire et al., 2017; Mochizuki et al., 2017). While the uptake of ozone inside a leaf leads to ROS production, isoprene reduces the amount of H_2O_2 formed in ozonized leaves (Loreto and Velikova, 2001), quenches singlet oxygen (Velikova et al., 2005a), and normalizes membrane stability in leaves recovering from ozone stress (Loreto et al., 2001; Loreto and Velikova, 2001). In addition, isoprene oxidation products, such as methyl vinyl ketone and methacrolein, have been detected to be directly emitted from oxidatively stressed leaves (Vollenweider et al., 2000; Oikawa and Lerdau, 2013; Cappellin et al., 2019), suggesting that isoprene oxidation occurs in leaves to remove ROS.

Because of the protective role of terpenoids emitted under ozone stress, ozone exposure would stimulate plants' terpenoid emissions (Rinnan et al., 2005). Previous studies have demonstrated that ozone damage is reduced considerably when isoprene is provided to

non-emitting plants, whereas leaf sensitivity to ozone increases and ozone damage is induced when isoprene synthesis is inhibited in isoprene emitters (Velikova et al., 2005a, 2005b; Loreto and Fares, 2007). Furthermore, H_2O_2 formation and lipid peroxidation are found to be reduced when isoprene is allowed to form (Glasauer and Chandel, 2013; Zhang et al., 2020). Moreover, a previous study demonstrated that long-term-adapted plants cannot respond to ozone stress by increasing their isoprene emission rates (Calfapietra et al., 2008). However, ozone tolerant clones can maintain higher isoprene emissions (Blande et al., 2007), and the capacity to maintain higher amounts of isoprene is an important factor in strengthening tolerance to ozone (Calfapietra et al., 2008). Despite accumulating laboratory and field studies on this aspect, there is inconsistency in ozone's effect on terpenoid emissions, probably arising not only from different plant species involved, but also from experimental designs and methods (e.g., ozone exposure design and terpenoid flux measurement technique). As shown in Fig. 2 and Table S1, while most studies have shown that ozone exposure has an inhibitory effect on isoprene emissions (Blande et al., 2007; Calfapietra et al., 2008; Li et al., 2009; Yuan et al., 2017b; Kanagendran et al., 2018), a few studies, however, revealed a promoting effect (Velikova et al., 2005b; Blande et al., 2007; Fares et al., 2008; Ryan et al., 2009; Kivimäenpää et al., 2013; Yuan et al., 2016, 2020) or no effect (Heiden et al., 1999; Blande et al., 2007; Calfapietra et al., 2008; Xu et al., 2012; Yuan et al., 2020). In contrast, more studies showed that ozone stress promotes monoterpene and sesquiterpene emissions (Heiden et al., 1999; Llusia et al., 2002; Blande et al., 2007; Behnke et al., 2009; Li et al., 2009; Loreto et al., 2004; Vitale et al., 2007; Carriero et al., 2016; Mochizuki et al. al., 2017; Kanagendran et al., 2018; Miyama et al., 2018; Brosset et al., 2020), yet some studies suggest suppression (Llusia et al., 2002, 2014; Kivimäenpää et al., 2013; Ghimire et al., 2017; Acton et al., 2018; Saunier and Blande et al., 2019; Brosset et al., 2020) or insignificant effects (Heiden et al., 1999; Peñuelas et al., 1999; Llusia et al., 2002; Blande et al., 2007; Behnke et al., 2009; Ghimire et al., 2017; Feng et al., 2018b; Brosset et al., 2020).

4. Elevated ozone and soil carbon

The plant carbon pool is an important part that connects the atmospheric carbon pool and soil carbon pool. Approximately 35–80% of the carbon fixed by plant photosynthesis is allocated to the underground ecosystem to maintain the continuous growth, death and renewal of the roots (Ryan and Law, 2005; Haverd et al., 2016). The carbon fixed

Fig. 2. A brief summary of the effects of elevated ozone on volatile emissions among different studies (The numbers in each bar indicates the total number of relevant published results).

through the plant by photosynthesis will be transferred into the soil carbon pool through the decomposition of roots and foliar litter. The soil-derived respiratory flux of CO_2 to the atmosphere is over ten times that of fossil fuel emissions (Gougoulias et al., 2014), thus even small changes in the soil carbon pool could significantly impact the atmospheric CO_2 pool (Lehmann and Kleber, 2015).

Ozone affects not only the above-ground part of the plant but also the below-ground part indirectly (McCrady and Andersen, 2000; Agathokleous et al., 2016). Reduced photosynthesis due to ozone exposure may result in decreased plant growth rates and overall productivity, thus finally impacting the carbon cycle of the soil (Loya et al., 2003). Leaves are the direct site of ozone action, determining the source supply of carbohydrate allocation to other plant parts (Andersen, 2003). Elevated ozone can modify resource allocation between above- (leave) and below-ground (root) parts of the plant, changing the pattern of plant carbon allocation, especially to the below-ground (King et al., 2001; McCrady and Andersen, 2000). As exposure to ozone causes physiological damage to vegetation, plants reduce carbon allocation to roots and even acquire carbon from roots due to the need for self-repair and antioxidant synthesis (Karlsson et al., 2003; Diaz-de-Quijano et al., 2012; Gerosa et al., 2015). However, the impact on the soil carbon cycle, as well as the underlying mechanisms, remain largely unclear (Qiu et al., 2021; Song et al., 2022).

Elevated ozone affects the quantity and quality of roots and foliar litter, altering the plant-soil-atmosphere carbon cycle (Agathokleous et al., 2016). Apart from the above-ground effects, ozone has the potential to alter below-ground processes and hence the carbon cycle in ways that are not currently being considered. Ozone triggers physiological changes in leaves that affect carbon source strength, leading to decreased carbon allocation below-ground and thus affecting roots and root symbionts (Kasurinen et al., 2005; Zeleznik et al., 2007). Ozone impacts carbon flux to soil mainly by altering rhizodeposition and leaf litter quantity/quality (Betzelberger et al., 2010) and by affecting plant-microbe interactions (Agathokleous et al., 2020), yet the magnitude and direction of the influence are plant-specific and depend on various environmental conditions. Meanwhile, current knowledge of ozone's impacts on plant-microbiota interactions and biodiversity is mainly limited to rhizosphere processes (Ueda et al., 2016; Trivedi et al., 2022), despite phylogenetically and functionally divergent microbiomes in different environments and climatic zones (Hacquard et al., 2015; Moore et al., 2015; Cordovez et al., 2019).

Elevated ozone appears to reduce the allocation of resources to roots more than to shoots; hence, the reduction of below-ground carbon allocation is usually accompanied by the reduction of the root-shoot ratio, but observed responses in the root-shoot ratio are highly variable owing to intra- and interspecies variation, culture conditions, and ontogenetic drift (Qiu et al., 2021). Plants tend to maintain the function of roots by reducing the quality and increasing the surface area (Luedemann et al., 2009; Diaz-de-Quijano et al., 2012). The turnover of fine roots is the main pathway for plants to transport carbon into the soil. However, there are only a few available studies on how ozone affects the dynamics of fine roots and the results are inconsistent: ozone may decrease (Kelting et al., 1995), increase (Kelting et al., 1995), or have no effect (Mainiero et al., 2009; Pregitzer et al., 2008) on the turnover of fine roots.

In addition, elevated ozone may also alter the quantity and quality of root exudates (Andersen, 2003). Elevated ozone reduces carbon allocation to the rhizosphere, leads to smaller root systems and possibly less extensive hyphal networks, which in turn changes the microbial communities in the rhizosphere, reduces soil carbon sequestration, and promotes the release of CO_2 to the atmosphere (Hu et al., 2018). Meanwhile, reducing carbon allocation to soil would induce less resources for heterotrophic microbes and thereby affect below-ground processes driven by microbes (Qiu et al., 2021). Elevated ozone may also alter the expression of microbial genes involved in carbon cycling, which in turn affects carbon cycling regulated by microbes (Levy-Booth
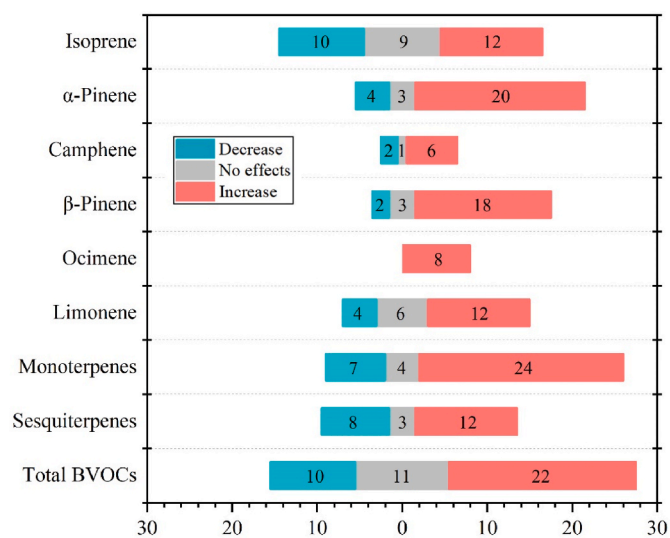
et al., 2014). A recent study indicated that although elevated ozone affected the bacterial community structure of the phyllosphere and the rhizosphere as a whole, this effect was relatively weak and did not lead to changes in the community function (Ueda et al., 2016). Nevertheless, numerous studies have demonstrated that the threats of elevated ozone significantly reduce soil organic carbon (Andersen, 2003; Loya et al., 2003; Qiu et al., 2021; Xia et al., 2021).

5. Elevated ozone and litter decomposition

Plant litter decomposition is another critical biogeochemical process that controls soil carbon dynamics in terrestrial ecosystems (Aragão et al., 2009; Beer et al., 2010). It sustains ecosystem productivity, and decomposition products enter the atmosphere in the form of CO_2 and enter the soil in the form of organic carbon (Chen et al., 2019). Elevated ozone alters plant carbon and nutrient distribution patterns, accelerates leaf senescence, and thereby changes the quantity and quality of foliar litter (Kasurinen et al., 2007, 2016; Meehan et al., 2010).

The effects of elevated ozone on litter decomposition rates have been investigated for several years (Parsons et al., 2004; Fierer et al., 2005; Knorr et al., 2005; Liu et al., 2005), but the effects seemed to vary with plant species and study locations (Booker, 2005; Kainulainen et al., 2003; Kasurinen et al., 2006; Parsons et al., 2004, 2008; Cornwell et al., 2008). The negative effects of ozone on the litter decomposition rate were obtained through meta-analysis, but the effects were different at different scales across plant species (Booker, 2005; Liu et al., 2009; Parsons et al., 2008; Baldantoni et al., 2011, 2013; Yue et al., 2015; Vitale et al., 2019). For instance, no apparent effects were found for the exposure studies of plants such as *Quercus ilex* L.*, Q. pubescens Wild., Q. robur* L.*, Pinus sylvestris* L. *and Betula papyrifera* (Kainulainen et al., 2003; Kasurinen et al., 2016; Vitale et al., 2019). Moreover, the ozone effects may vary in different litter decomposition stages. For example, Fu et al. (2018) found that elevated ozone reduced leaf litter decomposition at the early decomposition stage but slightly accelerated the decomposition of litter at the late stage, when investigating the exposure of *Ginkgo biloba* to elevated ozone.

The increased quantity of litter will strengthen the respiration of microorganisms, promote the decomposition of organic matter litter in the soil, and enlarge the flow of carbon from plants and soil to the atmosphere mainly through the emission of CO_2 (Cho et al., 2011; Hobley et al., 2014; Lehmann and Kleber, 2015; Kasurinen et al., 2016; Baldantoni et al., 2013). Thus, changes in litter quality due to elevated ozone will also influence litter decomposition and the soil organic matter budget (Meehan et al., 2010). Moreover, elevated ozone may affect phenolic compounds in leaves (Kasurinen et al., 2007), which are known to affect the nitrification, decomposition and nutrient recycling processes in soil, and the abundance and activity of the various soil biota (Hättenschwiler and Vitousek, 2000). In addition, elevated ozone alters nitrogen (N) cycling within leaves and promotes leaf N accumulation (Kasurinen et al., 2016; Stoelken et al., 2010), leading to increased N content and lowered C/N ratios, and thus speeding up the microbial decomposition of soil organic matter. Several studies have shown that elevated ozone increases the concentration of acid-soluble lignin (Kasurinen et al., 2006), but decreases the concentrations of nonstructural carbohydrates and soluble sugars in leaf litter (Booker, 2005; Fu et al., 2018).

6. Perspectives

Plants play a crucial role in the land-atmosphere interactions. The influence of human activities on the vegetation carbon pool comes not only from land-use changes, but also from climate and environmental changes. It is essential to assess plants' carbon sinks in a dynamic way under changing atmospheric compositions (e.g. CO_2 and oxidants) to achieve carbon neutrality goals. Although great efforts have been made to investigate the potential effects of elevated ozone on NPP and carbon

storage in terrestrial ecosystems, large uncertainties exist in the estimated effects either globally or regionally (Ren et al., 2007; Ainsworth et al., 2012; Xia et al., 2021). To narrow these uncertainties, more work is needed to more closely examine how ozone influences the plant-related carbon cycling processes, and to better understand the effects on the whole ecosystem in an integrated way.

- Previous studies have been conducted mostly in agricultural ecosystems with an overwhelming concern about crop yields. Due to the relatively more important role played by forests in carbon cycling, it is imperative to study ozone's impacts on forests, especially tropical and subtropical forests. Apart from controlled studies with seedlings, *in situ* studies under natural growing conditions are urgently needed, particularly long-term studies with a better representation of plant types, ages and nutrients, etc. Moreover, most field measurements document mainly the new plant biomass produced aboveground and therefore probably underestimate the belowground processes involving root exudates, litter decay, soil respiration, microbial activity and structure. Although root exudates, transfers to symbionts and losses to herbivores do not directly contribute to biomass increments, they may fuel other ecosystem processes such as decomposition, nutrient turnover and herbivory, and therefore are important parts influencing the overall carbon dynamics of ecosystems. In addition, while there are a few studies about the effects of elevated ozone on methane emissions from peatlands and wetlands (Mörsky et al., 2008; Toet et al., 2011; Williamson etal., 2016), studying the influence of ozone on methane exchange in forest ecosystems is warranted.
- Volatile emissions might be an insignificant part of plant-related carbon cycling. However, these highly reactive species play vital roles in atmospheric chemistry, including forming ozone and secondary organic aerosol, regulating atmospheric oxidation capacity (Lelieveld et al., 2008) and indirectly impacting radiative forcing (Harper and Unger, 2018). Therefore, volatile emissions represent a feedback from plants, and plants' responses to elevated ozone should be elucidated in an interactive way, taking into consideration this feedback, positive or negative, to the atmospheric environment.
- AOT40 (ozone concentrations accumulated over a threshold of 40 ppb) has been widely used to assess the potential effects of ozone on ecosystems and, in particular, crop yields. Fundamentally, it is the ozone taken up by plants (mainly by leaves), or internal ozone exposure, that truly matters. PODy (phytotoxic ozone dose above a threshold 'y', an index defining the amount of ozone entering the leaves through the stomata) was proposed to indicate plants' internal ozone exposure, and it is widely estimated based on stomatal conductance. However, this stomatal ozone flux is indeed less than the total ozone flux since ozone may also deposit on the surfaces of trunks, litters and soils. Measuring and/or estimating the total ozone flux above and below the canopy is a challenging task, and assessing ozone exposure doses for different ecosystem components would benefit from investigating various effects of ozone. Another concern is that ambient ozone has distinctive diurnal and seasonal variations. For example, a recent study demonstrated that ozone uptake at night is more damaging to plants than equivalent daytime flux (Goumenaki et al., 2021). Visser et al. (2021) suggested that ozone deposition impact assessments for forest canopies require accurate ozone flux partitioning on diurnal timescales. Therefore, night-time ozone effects should be further considered in future studies.
- In reality, many factors other than ozone, such as PAR, temperature, humidity and other atmospheric compositions (e.g., CO_2), may all impact plants and related carbon cycling processes. Although controlled studies have investigated the combined effects of ozone/ CO_2, ozone/soil moisture, and ozone/N-nutrient on crops or urban greening species, it is uncertain whether the combined effects can be applied to the more complex ecosystems (e.g., forests) and atmospheric compositions. In fact, many influencing factors are

interweaved and it is far from sufficient to document their effects with very limited controlled experiments for their simplified combinations (Niinemets et al., 2011; Zeng et al., 2022). Moreover, this interweaving influence may be further complicated by the fact that there are interactions among these factors. For example, PAR, temperature, and relative humidity may all individually impact plants, and they also influence ozone formation; therefore, it is difficult to single out the effects of ozone when the effects themselves are induced combinedly by many factors, and it is difficult to verify the effects as estimated in many model studies with observations. In the future, with extensive field observations, especially long-term observations in well-designed networks, may help to understand the effects under complex environments and facilitate deciphering the relationships, such that between NPP and ozone, using big data and artificial intelligence (AI) techniques.

- It is worth noting that there are other atmospheric oxidants other than ozone, such as OH radical, hydrogen peroxide (H_2O_2) and nitric acid (NO_3) radicals. OH and NO_3 radicals may play even more important roles than ozone in determining the lifetimes of trace gases in the atmosphere, although their mixing ratios are orders of magnitude lower. As measuring these radicals is still a formidable task, whether and how these oxidants affect plant physiology and carbon cycling will be a long-lasting challenge.
- The carbon neutrality goal is a spur to make clear carbon geochemical cycling on global, national and regional scales, especially natural carbon sequestration by terrestrial vegetation, since this would determine how much carbon responsibility a nation or region will resume to be carbon neutral for stabilizing and even diminishing the atmospheric carbon pool. This is the high time that geochemistry can help constrain the estimates with stable and radiocarbon isotopes (Affek and Yakir, 2003; Brueggemann et al., 2011; Bergman et al., 2021), and display skills such as molecular markers to indicate and trace the cycling or exchange processes.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apgeochem.2022.105400.

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Dr. Yanli Zhang is a professor in the State Key Laboratory of Organic Geochemistry at Guangzhou Institute of Geochemistry (GIG), Chinese Academy of Sciences (CAS). She got her Ph.D. degree at GIG in 2013 and then joined GIG as a research staff. She worked at the Hong Kong University of Science and Technology from 2017 to 2019 as a 'Hong Kong Scholar'. Her research interests are trace-level reactive organic gases (ROG) that directly and indirectly impact global and regional climate change, air quality, and ecosystem/human health. She is an Emerging Investigator of Applied Geochemistry/International Association of Geochemistry, recipient of NSFC Excellent Young Scientists Fund, a member of the Expert Group on China's Implementation of the Montreal Protocol on Ozone Depleting Substances, and an outstanding member of CAS Youth Innovation Promotion Association (YIPA).