Sensitivity of global greenhouse gas budgets to tropospheric ozone pollution mediated by the biosphere

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Abstract

Tropospheric ozone (O3), a harmful secondary air pollutant, can affect the climate via direct radiative forcing and by modifying the radiative forcing of aerosols through its role as an atmospheric oxidant. Moreover, O3 exerts a strong oxidative pressure on the biosphere and indirectly influences the climate by altering the materials and energy exchange between terrestrial ecosystems and the atmosphere. However, the magnitude by which O3 affects the global budgets of greenhouse gases (GHGs: CO2, CH4, and N2O) through altering the land–atmosphere exchange is largely unknown. Here we assess the sensitivity of these budgets to tropospheric O3 pollution based on a meta-analysis of experimental studies on the effects of elevated O3 on GHG exchange between terrestrial ecosystems and the atmosphere. We show that across ecosystems, elevated O3 suppresses N2O emissions and both CH4 emissions and uptake, and has little impact on stimulation of soil CO2 emissions except at relatively high concentrations. Therefore, the soil system would be transformed from a sink into a source of GHGs with O3 levels increasing. The global atmospheric budget of GHGs is sensitive to O3 pollution largely because of the carbon dioxide accumulation resulting from suppressed vegetation carbon uptake; the negative contributions from suppressed CH4 and N2O emissions can offset only ∼10% of CO2 emissions from the soil–vegetation system. Based on empirical data, this work, though with uncertainties, provides the first assessment of sensitivity of global budgets of GHGs to O3 pollution, representing a necessary step towards fully understanding and evaluating O3–climate feedbacks mediated by the biosphere.

1. Introduction

Tropospheric ozone (O3) is formed from the photochemical oxidation of carbon monoxide (CO) and volatile organic compounds (VOCs), typically initiated by the hydroxyl radical (OH), in the presence of nitrogen oxides (NOx ≡ NO+NO2) (Leighton 1961). Its concentration has significantly increased since the industrial revolution and is projected to either continue to rise or to decline over the course of this century with considerable spatial variability, driven largely by trends in fossil fuel combustion (source of NOx) and vegetation growth (source of VOCs) (Myhre et al 2013, Young et al 2013, Cooper et al 2014). In addition to severe damage to human health, what makes O3 particularly important as a pollutant in the troposphere is its reactivity with biochemical systems—it can alter the metabolisms involved with the production and/or consumption of radiatively significant gases such as CO2, CH4, and N2O (McLaughlin et al 2007, Zak et al 2011, Ainsworth et al 2012, Agathokleous et al 2016). All of these could largely contribute to changes in the atmospheric GHG budgets and affect climate (Stitch et al 2007). This paper provides the first assessment of the sensitivity of global budgets of CO2, CH4, and N2O to tropospheric O3 abundance resulting from the alterations of land-atmosphere exchange based on a meta-analysis of published experimental studies of O3 impacts on the exchange of these three gases from varying ecosystems.
There are a myriad of mechanisms at different organizational levels by which the oxidizing capacity of O₃ affects terrestrial ecosystems. Ozone can directly depress photosynthesis by disturbing cellular biochemistry or indirectly by damaging stomatal function; in either case it alters carbon and water exchange (Ainsworth et al. 2012). Ozone can also change secondary metabolism and tissue chemistry, which can affect carbon mineralization (Findlay et al. 1996, Loya et al. 2003, Valkama et al. 2007). At the community level, O₃ exerts indirect effects on species composition through mediation of competitive relations (Wang et al. 2016). Since O₃ does not penetrate soil (Blum and Tingey 1977), impacts on the processes responsible for the production and/or consumption of CO₂, CH₄, and N₂O in soils are mediated by these aboveground changes (figure 1). Changes in organic matter production, composition, and allocation, in turn, affect decomposition and carbon and nitrogen cycling, and alter rates of CO₂ and N₂O production and CH₄ production/consumption (Agathokleous et al. 2016).

Independent empirical studies from different ecosystems around the world have been conducted to measure changes in the sources or sinks of GHGs in response to elevated O₃. These experiments feature different designs with regards to ecosystem type, fumigation method and duration, O₃ manipulation level, and other experimental factors (e.g. atmospheric CO₂ level). Such differences likely contribute to inconsistencies among different studies and complicate efforts to synthesize and interpret the results. Here, we conducted a meta-analysis (Hedges et al. 1999, Gurevitch et al. 2001) of the published literature to statistically synthesize and analyze all reported empirical findings and determine the sensitivity of CO₂, CH₄, and N₂O exchange between terrestrial ecosystems and the atmosphere to changes in O₃ pollution. These results allow for the first systematic assessment of the sensitivity in the budgets of GHGs to tropospheric O₃ concentration elevation that are based on empirical data.

2. Methods

2.1. Data collection

A search of published literature concerning O₃ influences on belowground processes was initially conducted in both the ISI Web of Science (Thomson Reuters, New York, NY, USA) and Google Scholar.
of which the sampling variance was computed by:

\[ v = \frac{(SD_t)^2}{N_t(X_t)^2} + \frac{(SD_c)^2}{N_c(X_c)^2} \]  

(2)

where \( X_t \) is the control mean, \( X_t \) is the treatment mean, \( SD_t \) is the control standard deviation, \( SD_c \) is the treatment standard deviation, \( N_t \) is the control replication number, and \( N_c \) is the treatment replication number.

The normalization of effect sizes under different \( O_3 \) manipulation levels to a same \( \Delta O_3 \) followed a linear transformation procedure:

\[ X_{nl} = X_c + \left( \frac{X_t - X_c}{\Delta O_3} \right) \Delta CO_3^* \]  

(3)

where \( X_{nl} \) is the normalized value, \( X_c \) is the control mean, \( X_t \) is the treatment mean, \( \Delta O_3 \) is the \( O_3 \) level difference between the treatment and control, and \( \Delta CO_3^* \) represents the \( O_3 \) level difference to which the effect sizes are normalized (i.e. a certain \( O_3 \) concentration interval between the current troposphere \( O_3 \) level and an elevated \( O_3 \) level: 10, 20, 30 and 40 ppb).

Meta-analysis of RR was performed by fitting to the random-effects model via the restricted maximum-likelihood (REML) method. The inverse-variance weighted mean of RRs and the standard error of the random-effects model via the restricted maximum-likelihood (REML) method. The inverse-variance weighted mean RR for each level was calculated. An omnibus test was further conducted, indicating that the mean RR differed among the levels of this categorical moderator.

The meta-regression of RR with moderators was performed by fitting to the mixed-effects model via the REML method as well. An omnibus test with a chi-square distribution (Q\( M_\beta \)) was conducted to show whether the moderator has a significant contribution to the total heterogeneity. For categorical moderator with a significant Q\( M_\beta \), the categorical group was subdivided and the inverse-variance weighted mean RR for each level was calculated. An omnibus test was further conducted, with a significance of Q\( M_\beta \) indicating that the mean RR were different among the levels of this categorical moderator.

In addition, during the meta-analysis publication bias was tested by funnel plots (Jennions et al 2013), and Egger’s regression test was further performed to test the plot asymmetry (Egger et al 1997). Q-Q normal plots were created to test whether the effect sizes fulfill the normality requirement (Wang and Bushman 1998). All calculation procedures described above were executed by R language using the ‘metafor’ package (Viechtbauer 2010).
2.3. Estimation of global GHG budget sensitivity

The meta-analysis results provide the average changes of each gas across the terrestrial ecosystems over the planet under a certain O₃ concentration interval between the current troposphere O₃ level and an elevated O₃ level (i.e. \( \Delta O_3 \) in ppb). We can give an approximate sensitivity estimate of the global GHG changes in response to this tropospheric O₃ level increase relative to today in a way as follows:

\[
\Delta F = F'_c \Delta A
\]

where \( \Delta F \) change (year⁻¹) represents the average change of each flux; \( F'_c \) (year⁻¹) represents the strength of each flux under the current O₃ level; and \( \Delta A \) (%), obtained from meta-analysis and dependent on O₃ level, denotes the average percentage change of each flux. The current strengths of the different fluxes are listed in table S1 in supporting information S2. It is noteworthy that the upscaling here has integrated the major ecosystem types, though still not yet a complete representation, across the land surface. This representativeness is much better than the previous global modelling studies that parameterized O₃ effects in global ecosystem models with strikingly limited O₃ response data. For example, in the study of O₃ impacts on global carbon cycling by Sitch et al (2007) O₃ response data for only a few European and North America species were extrapolated to represent all global vegetation types.

As for the determination of net flux of CO₂ into the atmosphere, our work only conducted a meta-analysis of soil respiration and thus the change in carbon uptake by terrestrial vegetation is necessary to complete the analysis. Previous meta-analysis of plant photosynthesis response to O₃ elevation for trees (Wittig et al 2007), wheat (Feng et al 2008), and soybeans (Morgan et al 2003), and studies comparing plants from multiple functional groups find a consistent 20% reduction (Reich and Amundson 1985, Volin et al 1998, Lombardozzi et al 2015). Moreover, the synthesis work by Lombardozzi et al (2013) did not find a significant correlation between photosynthesis response and O₃ level and agreed with the average 20% effect. Therefore, a constant 20% value is applied to constrain the global net primary productivity (NPP) to quantify the reduction of vegetation carbon uptake caused by different O₃ elevation levels. It is noteworthy that our meta-analysis of soil respiration also includes the autotrophic respiration by plant roots, which, however, is not included in the NPP term. This represents a small uncertainty. Note that for the CO₂ flux change a 50% reduction is further applied assuming 50% percent of the net accumulation of CO₂ from the terrestrial biosphere is sequestered by the ocean (Sabine et al 2004).

To describe the global GHG budget change, GWP (global warming potential) was used to calculate the GHG balance in units of CO₂ equivalents as follows:

\[
GHG = F_{CO_2-C} * 44/12 + F_{CH_4-C} * 16/12
+ GWP_{CH_4} + F_{N_2O-N} * 44/28 * GWP_{N_2O}
\]

where \( F_{CO_2-C} \), \( F_{CH_4-C} \), and \( F_{N_2O-N} \) are annual changes of total soil CO₂ efflux, N₂O, and CH₄ as calculated by the above equation. The fractions 44/12 and 44/28 were used to convert the mass of CO₂-C, CH₄-C, and N₂O-N into CO₂, CH₄, and N₂O. GWP_{CH_4} (Pg CO₂ equivalent (equiv.) per Pg CH₄) and GWP_{N_2O} (Pg CO₂ equiv. per Pg N₂O) are constants indicating integrated radiative forcing of CH₄ (28) and N₂O (265) in terms of a CO₂ equivalent unit over a period of 100 years (Caissi et al 2013).

3. Results

Collectively, 96 effect sizes (RRs) for soil respiration (CO₂ emission), N₂O emission, and CH₄ emission and uptake were compiled from peer-reviewed studies (supporting information S1). These studies were conducted in the Northern Hemisphere for ecosystems including forest, grassland, agricultural land, and peat land (figure S1 in supporting information S2). The data do not show publication bias based on funnel plots and Egger’s tests (figure S2 supporting information S2) and fulfill the requirement of normality according to Q-Q plots (figure S3 in supporting information S2). Moreover, methodological differences, i.e. fumigation method and duration, among studies do not make a significant contribution to RR variability, with the exception of fumigation method for CH₄ emission (table S2 in supporting information S2). For these reasons, we conducted the analyses across the entire dataset.

Differing O₃ manipulation levels were adopted by different studies. We choose the absolute difference in experimental O₃ concentration between the treatment and control (hereafter referred to as \( \Delta O_3 \)) as a variable to describe the different studies. Meta-regressions between \( \Delta O_3 \) and RR of different gases indicate that the RR of CO₂ and CH₄ (both emission and uptake) hold a significantly positive and negative linear relationship with \( \Delta O_3 \), respectively, while the RR of N₂O is uncorrelated with \( \Delta O_3 \) (figure 2). These results suggest that the magnitude of CO₂ and CH₄ responses depend on O₃ levels in the lower atmosphere. As for N₂O, based on limited data we cannot exclude its dependence on O₃ levels. In this study, we temporarily treat N₂O response as being independent O₃ level. Therefore, to assess the sensitivity of terrestrial ecosystems in terms of GHG exchange to O₃ pressure, we tested four \( \Delta O_3 \) levels—10, 20, 30, and 40 ppb—to which RR were linearly normalized, except for N₂O. Meta-analyses were further conducted on these normalized RR.

First, GHGs from different ecosystems present differing sensitivities to changes in O₃ (table S3 in
supporting information S2). The CO2 effluxes from soils in both cropland and peatland, though with a similar magnitude, show a low sensitivity to increased O3 (figure S4 in supporting information S2). By contrast, CO2 effluxes from grassland soils display strong sensitivity to elevated O3, with CO2 flux diminished by from more than 10% (10 ppb) to more than 60% (20 ppb), and the forest shows a smaller but still significant response of 5% (10 ppb) to 30% (40 ppb) (figure S4 in supporting information S2). For CH4 emissions, rice paddies present a significant reduction from almost 7% (10 ppb) to 25% (40 ppb), while the peat land does not show significant responses to O3 elevation (figure S5 in supporting information S2). Similarly, O3 enrichment shows a significantly different effect on the N2O flux among the three ecosystems as well. Elevated O3 results in a reduction of N2O emissions by an average of 19% (statistically not significant), 16%, and 41% for cropland, rice paddies, and grassland, respectively (figure S6 in supporting information S2). Additionally, this meta-analysis indicates that O3 and CO2 elevations in combination have a larger influence on CO2 and N2O effluxes than O3 alone (figures S4, S6 in supporting information S2). This may result from a carbon fertilization effect and associated protection of carbon fixation against elevated O3 via stomatal closure (Sitch et al 2007, Valkama et al 2007).

Integrating the responses across these different ecosystems, we derived the average responses for each gas. For soil CO2 efflux, the RR of CO2 is positively correlated with O3 level (figure 2(a)), but does not show a significant sensitivity to O3 enrichment until ΔO3 of 30 and 40 ppb, when soil respiration is stimulated by an average of about 12% and 15%, respectively (figure 3(a)). By contrast, CH4 emissions are sensitive to O3 across the full range of treatments, with an average of 6% (10 ppb), 11% (20 ppb), 14%

Figure 2. Meta-regression between RR and ΔO3. (a)–(d) denote soil respiration, CH4 emission, CH4 uptake, and N2O emission, respectively. The RR of N2O is not statistically correlated with ΔO3 (d). The size of the bubble is the relative weight of the RR in the random-effects meta-regression. Larger bubbles indicate study outcomes that contributed a greater overall weight in meta-regressions.
and 16% (40 ppb) (figure 3(b)). Similarly, CH$_4$ uptake is sensitive to the dose of elevated O$_3$ with a large reduction seen initially but with low sensitivity to further increases in O$_3$ (figure 3(c)). Finally, the RR of N$_2$O emissions does not depend on O$_3$ manipulation level (figure 2(d)); elevated O$_3$ significantly decreases N$_2$O emission by an average of 22% regardless of the O$_3$ level (figure 3(d)). Our meta-analysis suggests that the soil respiration of terrestrial ecosystems is rather insensitive to O$_3$ pressure, stimulating CO$_2$ release to the atmosphere only after large O$_3$ changes. These responses of CO$_2$, CH$_4$, and N$_2$O exchange occur primarily because of reduced carbon availability from inhibited photosynthesis and slower decomposition and nitrogen return from altered detritus quality (Findlay et al 1996, Andersen 2003, Grantz et al 2006, Kanerva et al 2006). However, it has also been postulated that O$_3$ pressure may stimulate mycorrhizal formation in fine roots and root nutrient acquisition and turnover (Scagel and Andersen 1997, Kasurinen et al 2004) or greater consumption of the carbon formed since the O$_3$ pressure because of changes in microbial activity and carbon quality (Loya et al 2003), which cause unsuppressed and even enhanced CO$_2$ efflux from soils.

Scaling up these average ecosystem-scale responses, we estimate the sensitivity of global budget of the three gases to enhanced O$_3$ (figure 4) As shown in figure 4(a), the contribution by suppressed N$_2$O flux to the global budget is consistently $\sim$1.23 Pg CO$_2$ equiv. yr$^{-1}$. Increased O$_3$ of 10 and 20 ppb induce a decline of the current terrestrial natural CH$_4$ emission flux by an average of 6% and 11%, which contributes

![Figure 3. Meta-analysis of GHGs exchange across different ecosystems. (a)–(d) shows the meta-analysis results of soil respiration (a), CH$_4$ emission (b), CH$_4$ uptake (c), and N$_2$O emission (d) respectively, with mean and 95% confidence interval. The values are back-transformed from the RRs. The response is significant if the interval does not overlap 1 (denoted by the dashed line). Values presented in this figure minus 1 multiplied by 100 correspond to the % change, with the negative and positive suggesting a decrease and an increase, respectively. Values listed on the bar are the mean of significant responses.](image-url)
O3-induced net increase of CO2 (
productivity to elevated O3 predominate the global
Therefore, the sensitivity of terrestrial vegetation
consideration O3-suppressed CO2 uptake by vegeta-
tropospheric O3 pollution, and signi
ecosystems and the atmosphere is sensitive to
Overall exchange of GHGs between terrestrial
into a source with O3 level continuously increasing
that the soil system can be transformed from a sink
GHGs budget change on average is approximately 21.0
co
1. Global soil CO2 ef
ux (Tg CO2/yr)

Figure 4. Sensitivity of global GHG budget change to O3 change. (a) Shows the positive (enhanced soil respiration and suppressed CH4 uptake) and negative contributions (suppressed N2O and CH4 emissions) to the atmospheric GHGs. (b) Shows the net global budget change and the percent of positive contributions offset by the negative contributions by accounting for the positive contribution from suppressed vegetation carbon uptake (that is, 22.0 Pg C yr⁻¹). All values are in CO2 equiv. See table S4 in supporting information S2 for specific calculation and data source.

First, GHGs from different ecosystems present differing sensitivities to changes in O3 due to fundamental differences in vegetation composition. However, this study, as a pioneering work, integrates the different systems in an aggregate way, using the average responses disregarding the variations (though they are small relative to the sensitivities themselves). Moreover, uncertainties in the baseline estimates of the GHG fluxes will necessarily increase the magnitude of uncertainty of GHG fluxes sensitivity to O3 exposure. Ecosystem-specific assessments are expected for future studies to tackle these uncertainties. A related question that should be addressed involves the impact of using different measures of O3 dosage (e.g. AOT40 and O3 flux) rather than O3 concentration on estimates of ecosystem sensitivity. Second, the studied ecosystem types and independent observations that can be included in this meta-analysis are limited. For example, upland forest ecosystems generally act as a sink of CH4 (e.g. Yavitt et al 1990), but no study is
current available of the O$_3$-sensitivities of these ecosystems. There is also a striking lack of experimental data from the Southern Hemisphere (figure S1 in supporting information S2). This problem is particularly important because many regions in the Southern Hemisphere are predicted to industrialize in the future, which could lead to higher O$_3$ levels in the vicinity of cities and hemisphere-wide. Clearly, more field measurements on CO$_2$, N$_2$O, and CH$_4$ fluxes around the world should be undertaken. Third, exchange of GHGs between the atmosphere and terrestrial ecosystems can be simultaneously influenced by other global change agents. To more fully and realistically evaluate O$_3$ impacts on GHGs, the combined impacts with other global change agents, e.g. nitrogen deposition and climate warming, need additional investigation.

5. Conclusion

By fully accounting for the three gases simultaneously, we find that with the O$_3$ level continuously increasing the whole soil system would be transformed from a sink into a source of GHGs. With an increase of O$_3$ concentration by 10 ppb, the global annual net atmospheric budgets would on average increase by $\sim$12% (i.e. $\sim$5 Pg C yr$^{-1}$). However, in the global atmospheric budget suppressed CH$_4$ and N$_2$O emissions can offset a small portion (at most 10%) of the net CO$_2$ increase derived from changes in soil respiration and vegetation carbon fixation in terms of CO$_2$-equivalent. The sensitivity of global net GHGs budgets is still predominantly determined by the high sensitivity and thus a large magnitude of O$_3$-induced reduction in terrestrial vegetation carbon sequestration capability.

Natural systems with a high biodiversity, however, are increasingly suggested to be resilient to O$_3$ pressure. For example, the productivity and carbon stock of the temperate deciduous forest in the Eastern United States are shown to be unsuppressed by O$_3$ pressure (Wang et al 2016). The FACE study by Zak et al (2011), which included both O$_3$-tolerant and O$_3$-sensitive species or genotypes, also indicated unsuppressed net primary productivity after a long-term fumigation (11 years). Grassland ecosystems including temperate (Volk et al 2011), calcareous (Thwaites et al 2006), and alpine types (Bassin et al 2007) have also shown that the productivity is insensitive to elevated O$_3$. Hence, we postulate that the indirect role of O$_3$ (that is via altering the land–atmosphere exchange) on the Earth’s radiative balance might be most significant on those managed systems that are of low diversity, e.g. agricultural and forest plantation systems. This means agricultural production practices would play a key role in mitigating O$_3$’s indirect effects on global climate, reinforcing the conclusion that adoption of best practices in human-impacted ecosystems could mitigate climate change (Paustian et al 2016, Tian et al 2016).

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References

Agathokleous E, Saitanis C J, Wang X, Watanabe M and Koike T 2016 A review study on past 40 years of research on effects of tropospheric O$_3$ on belowground structure, functioning, and processes of trees: a linkage with potential ecological implications Water Air Soil Pollut. 227 1–28
Ainsworth E A, Yendrek C R, Stitch S, Collins W J and Emberson L D 2012 The effects of tropospheric ozone on net primary productivity and implications for climate change Annu. Rev. Plant Biol. 63 637–61
Andersen C P 2003 Source–sink balance and carbon allocation below ground in plants exposed to ozone New Phytol. 157 213–28
Bassin S, Volk M, Suter M, Buchmann N and Fuhrer J 2007 Nitrogen deposition but not ozone affects productivity and community composition of subalpine grassland after 3 yr of treatment New Phytol. 175 523–34
Blum U and Tingey D T 1977 A study of the potential ways in which ozone could reduce root growth and nodulation of soybean Atmos. Environ. 11 757–79
Ciais P et al 2013 Climate change 2013: the physical science basis Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change ed T F Stocker et al (Cambridge University Press) pp 465–570 ch 6
Cooper O R et al 2014 Global distribution and trends of tropospheric ozone: an observation-based review Elementa: Sci. Anthropocene 2 00029
Egger M, Smith G D, Schneider M and Minder C 1997 Bias in meta-analysis detected by a simple, graphical test BMJ 315 629–34
Feng Z, Kobayashi K and Ainsworth E A 2008 Impact of elevated ozone on belowground structure, functioning, and yield of wheat (Triticum aestivum L.): a meta-analysis Glob. Change Biol. 14 2696–708
Findlay S, Carreiro M, Kirschik V and Jones C G 1996 Effects of damage to living plants on leaf litter quality Ecol. Appl. 6 269–75
Gurevitch J, Curtis P S and Jones M H 2001 Meta-analysis in ecology Adv. Ecol. Res. 32 199–247
Gratzl D, Guen S and Vu H B 2006 O$_3$ impacts on plant development: a meta-analysis of root/shoot allocation and growth Plant Cell Environ. 29 1193–209
Hedges L V, Gurevitch J and Curtis P S 1999 The meta-analysis of response ratios in experimental ecology Ecology 80 1150–6
Hickman J E, Wu S, Mickley L J and Lerdau M T 2010 Kadzu (Pueraria montana) invasion doubles emissions of nitric oxide and increases ozone pollution Proc. Natl Acad. Sci. 107 10115–9
Jennions M D, Lortie C J, Rosenberg M S and Rothstein H R 2013 Publication and related biases Handbook of Meta-analysis in Ecology and Evolution ed J Koricheva, J Gurevitch and K Mengersen (Princeton, NJ: Princeton University Press) pp 207–236
Kanerva T et al 2006 A 3 year exposure to CO2 and O3 induced minor changes in soil N cycling in a meadow ecosystem Plant Soil 286 61–73
Kasurinen A, Kokko-Gonzales P, Riikonen J, Vapaavuori E and Holopainen T 2004 Soil CO2 efflux of two silver birch clones exposed to elevated CO2 and O3 levels during three growing seasons Glob. Change Biol. 10 1654–65
Koricheva J, Gurevitch J and Mengersen K 2013 Handbook of Meta-analysis in Ecology and Evolution (Princeton: Princeton University Press)
Leighton P A 1961 Photochemistry of Air Pollution (New York: Academic)
Lombardozzi D, Levis S, Bonan G, Hess P and Sparks J 2015 The influence of chronic ozone exposure on global carbon and water cycles J. Clim. 28 292–305
Lombardozzi D, Sparks J P and Bonan G 2013 Integrating O3 influences on terrestrial processes: photosynthetic and stomatal response data available for regional and global modeling Biogosciences 10 6813–83
Loya W M, Pregitzer K S, Karberg N J, King J S and Giardina C P 2003 Reduction of soil carbon formation by tropospheric ozone under increased carbon dioxide levels Nature 425 705–7
McLaughlin S B, Wullschleger S D, Sun G and Nosal M 2007 Interactive effects of ozone and climate on water use, soil moisture content and streamflow in a southern Appalachian forest in the USA New Phytol. 174 125–36
Morgan P, Ainsworth E and Long S 2003 How does elevated ozone impact soybean? A meta-analysis of photosynthesis, growth and yield Plant Cell Environ. 26 1317–28
Myhre G et al 2013 Anthropogenic and natural radiative forcing Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change ed T F Stocker, D Qin, G K Plattner, M Tignor, S K Allen, J Boschung, A Nauels, Y Xia, V Bex and P M Midgley (Cambridge: Cambridge University Press) pp 659–740
Paustian K et al 2016 Climate-smart soils Nature 532 49–57
Reich P B and Amundson R G 1985 Ambient levels of ozone reduce net photosynthesis in tree and crop species Science 230 566–70
Sabine C L et al 2004 The oceanic sink for anthropogenic CO2 Science 305 367–71
Scagel C F and Andersen C P 1997 Seasonal changes in root and soil respiration of ozone-exposed ponderosa pine (Pinus ponderosa) grown in different substrates New Phytol. 136 627–43
Sitch S, Cox P, Collins W and Huntingford C 2007 Indirect radiative forcing of climate change through ozone effects on the land-carbon sink Nature 448 791–4
Thwaites R, Ashmore M, Morton A and Pakeman R 2006 The effects of tropospheric ozone on the species dynamics of calcareous grassland Environ. Pollut. 144 500–9
Tian H et al 2016 The terrestrial biosphere as a net source of greenhouse gases to the atmosphere Nature 531 233–8
Valkama E, Koricheva J and Oksanen E 2007 Effects of elevated O3 alone and in combination with elevated CO2 on tree leaf chemistry and insect herbivore performance: a meta-analysis Glob. Change Biol. 13 184–201
Viechhauer W 2010 Conducting meta-analyses in R with the metafor package J. Stat. Softw. 36 1–48
Volin J C, Reich P B and Giovincii T J 1998 Elevated carbon dioxide ameliorates the effects of ozone on photosynthesis and growth: species respond similarly regardless of photosynthetic pathway or plant functional group New Phytol. 138 315–25
Volk M et al 2011 Subalpine grassland carbon dioxide fluxes indicate substantial carbon losses under increased nitrogen deposition, but not at elevated ozone concentration Glob. Change Biol. 17 366–76
Wang B, Shugart H H, Shuman J K and Lerdau M T 2016 Forests and ozone: productivity, carbon storage, and feedbacks Sci. Rep. 6 22133
Wang M C and Bushman B J 1998 Using the normal quantile plot to explore meta-analytic data sets Psychol. Meth. 3 46
Wittig V E, Ainsworth E A and Long S P 2007 To what extent do current and projected increases in surface ozone affect photosynthesis and stomatal conductance of trees? A meta-analytic review of the last 3 decades of experiments Plant Cell Environ. 30 1150–62
Yavitt J B, Downey D M, Lang G E and Saxstone A J 1990 Methane consumption in two temperate forest soils Biogeochemistry 9 39–52
Young P J et al 2013 Pre-industrial to end 21st century projections of tropospheric ozone from the Atmospheric Chemistry and Climate Model Intercomparison Project (ACCMIP) Atmos. Chem. Phys. 13 2063–90
Zak D R, Pregitzer K S, Kubiske M E and Burton A J 2011 Forest productivity under elevated CO2 and O3: positive feedbacks to soil N cycling sustain decade-long net primary productivity enhancement by CO2 Ecol. Lett. 14 1220–6