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# Stomatal conductance influences interannual variability and long-term changes in regional cumulative plant uptake of ozone

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Supplementary material for this article is available [online](#)

## Abstract

Ambient ozone uptake by plant stomata degrades ecosystem and crop health and alters local-to-global carbon and water cycling. Metrics for ozone plant damage are often based solely on ambient ozone concentrations, overlooking the role of variations in stomatal activity. A better metric is the cumulative stomatal uptake of ozone (CUO), which indicates the amount of ozone entering the leaf over time available to cause physiological damage. Here we apply the NOAA GFDL global earth system model to assess the importance of capturing interannual variations and 21st century changes in surface ozone versus stomatal conductance for regional mean CUO using 20-year time-slice simulations at the 2010s and 2090s for a high-warming climate and emissions scenario. The GFDL model includes chemistry-climate interactions and couples atmospheric and land components through not only carbon, water, and energy exchanges, but also reactive trace gases—in particular, ozone dry deposition simulated by the land influences surface ozone concentrations. Our 20-year time slice simulations hold anthropogenic precursor emissions, well-mixed greenhouse gases, and land use distributions fixed at either 2010 or 2090 values. We find that CUO responds much more strongly to interannual and daily variability in stomatal conductance than in ozone. On the other hand, long-term changes in ozone explain 44%–90% of the annual CUO change in regions with decreases, largely driven by the impact of 21st century anthropogenic NO<sub>x</sub> emission trends on summer surface ozone. In some regions, increases in stomatal conductance from the 2010s to 2090s counteract the influence of lower ozone on CUO. We also find that summertime stomatal closure under high carbon dioxide levels can offset the impacts of higher springtime leaf area (e.g. earlier leaf out) and associated stomatal conductance on CUO. Our findings underscore the importance of considering plant physiology in assessing ozone vegetation damage, particularly in quantifying year-to-year changes.

## 1. Introduction

Plant stomata control the uptake of carbon dioxide for photosynthesis and release of water vapor into the atmosphere through transpiration. Ambient ozone diffuses through open stomata and reacts quickly with fluids and tissues once inside the leaf (Laisk *et al* 1989, Wang *et al* 1995). Stomatal uptake of ozone serves as an important removal pathway of tropospheric ozone (Wesely and Hicks 2000, Fowler *et al* 2009, Clifton *et al* 2020a), which is a potent greenhouse gas, air

pollutant, and a strong lever on the atmospheric oxidation capacity. Oxidation inside the leaf following stomatal ozone uptake causes cell death and decreases carbon fixation, leading to necrosis, reduced ecosystem productivity and carbon storage over time (Fiscus *et al* 2005, Ainsworth *et al* 2012), and lost crop yields (Mauzerall and Wang 2001, Morgan *et al* 2003, Feng *et al* 2008, Tai *et al* 2014, McGrath *et al* 2015). By changing local-to-global carbon cycling as well as altering energy and water exchanges, stomatal ozone uptake influences meteorology, climate, and

air quality (Sitch *et al* 2007, Lombardozzi *et al* 2015; Super *et al* 2015, Li *et al* 2016, 2018, Sadiq *et al* 2017, Zhou *et al* 2018).

Changes in ecosystem functioning and land-atmosphere exchanges due to ozone plant damage depend on the cumulative stomatal uptake of ozone (CUO) (e.g. Musselman *et al* 2006). While the argument for including CUO in ozone plant damage metrics is decades old (Reich 1987, Musselman and Massman 1999, Matyssek *et al* 2004, Paoletti and Manning 2007), damage or risk is often evaluated based solely on metrics of ambient ozone concentrations (McLaughlin *et al* 2007, Hollaway *et al* 2012, Sun *et al* 2012, Tai *et al* 2014, Lapina *et al* 2014, 2016, Mills *et al* 2018) given the paucity of observational constraints on CUO. Recent work, leveraging a gridded surface ozone observational product (Schnell *et al* 2014) and observed water fluxes from tower sites (Pastorello *et al* 2017), highlights the limitations of concentration-based metrics in capturing interannual and spatial variations in CUO across 100+ sites in the United States and Europe (Ducker *et al* 2018), in agreement with the findings of work at individual sites (e.g. Gerosa *et al* 2004) and modeling studies (Mills *et al* 2011, De Marco *et al* 2015, Anav *et al* 2016).

Ozone damage to plants depends not only on CUO but also on the plants' ability to detoxify and respond to ozone (Musselman and Massman 1999, Massman *et al* 2000, Musselman *et al* 2006, Paoletti and Manning 2007, Matyssek *et al* 2008). For example, plants scavenge some of the ozone inside the leaf such that a certain amount of ozone does not pose a risk to the plant other than by depleting detoxification reserves. Detoxification has been shown to depend on environmental conditions and species (e.g. Musselman *et al* 2006), and recently on the ratio of dry leaf mass to leaf area in woody plants (Feng *et al* 2018), but is highly uncertain, especially at regional scales (Karnosky *et al* 2007, Lombardozzi *et al* 2015, Jolivet *et al* 2016).

Parameterizations that include plant detoxification and responses to ozone in regional-to-global models are used to assess the impacts of CUO on crop yields, carbon and water cycling, climate, and air quality (Sitch *et al* 2007, Lombardozzi *et al* 2015, 2018, Li *et al* 2016, 2018, Sadiq *et al* 2017, Oliver *et al* 2018, Arnold *et al* 2018, Unger *et al* 2020, Lei *et al* 2020). Most studies employing damage parameterizations in large-scale models probe either the carbon and water cycling impacts of 'turning on' schemes, or the impacts of changes in either surface ozone or stomatal conductance ( $g_s$ ). While some of these studies examine the impacts of changes in both ozone and  $g_s$ , they do not separate how changes in ozone versus  $g_s$  drive the changes in impacts.

Because surface ozone and  $g_s$  both influence CUO but respond to meteorology and the land surface differently, there may be individual changes in ozone and  $g_s$  that counteract and limit, or compound and

amplify, changes in CUO. Indeed Ronan *et al* (2020) use the Ducker *et al* (2018) CUO dataset to illustrate that recent reductions in ozone air pollution at sites in the US and Europe due to  $\text{NO}_x$  ( $= \text{NO} + \text{NO}_2$ ) emission controls do not benefit plants due to offsetting increases in  $g_s$ . Other work modeling CUO suggests counteracting changes in  $g_s$  and surface ozone on CUO at present day (Anav *et al* 2019) and by the end of the 21st century (Klingberg *et al* 2011) over Europe. These studies use uncoupled modeling frameworks, where meteorology from a regional climate model is fed into a regional chemical transport model and  $g_s$  used for CUO is inconsistent with  $g_s$  used for determining ambient ozone through dry deposition as well as with  $g_s$  used for energy and water exchanges. Here, we use a new version of a global earth system model with chemistry-climate interactions and self-consistent land-atmosphere exchanges of carbon, water, heat, and reactive gases including ozone (Paulot *et al* 2018, Clifton *et al* 2020b) to explore the roles of surface ozone versus  $g_s$  in driving interannual and long-term variability in CUO. In particular, we show a critical role for interannual variations and 21st century changes in  $g_s$  on regional mean CUO.

## 2. Methods

We use the NOAA GFDL global chemistry-climate model AM3, which includes stratosphere-troposphere gas-phase and aerosol chemistry (Donner *et al* 2011, Naik *et al* 2013). AM3 is the atmospheric component of the fully coupled atmosphere-ocean general circulation model CM3, which was used and evaluated extensively in the 5th phase of the Coupled Model Intercomparison Project (CMIP5). The underlying land surface model of AM3/CM3 is LM3 (Shevliakova *et al* 2009, Milly *et al* 2014), which includes water, energy, and carbon cycling, vegetation dynamics and land use and management, and is coupled to atmospheric dynamics and radiation via surface albedo, surface roughness, and exchanges of water, energy, and momentum. We use a new version of AM3 called AM3DD where the land and tropospheric chemistry are coupled through dry deposition of reactive gases like ozone (Paulot *et al* 2018, Clifton *et al* 2020b). Because AM3 and LM3 are fully coupled, we refer to the GFDL model as an earth system model (note that we reduce computational expense by forcing sea surface temperatures and sea ice).

We examine time-slice AM3DD simulations of RCP8.5 at the 2010s and 2090s. RCP8.5 is an emissions and climate scenario designed by CMIP5 for the IPCC Fifth Assessment Report (Moss *et al* 2010, van Vuuren *et al* 2011). Each AM3DD simulation contains 20 years. Well-mixed greenhouse gases are prescribed at 2010 and 2090 values for the 2010s and

2090s simulations, respectively, and sea surface temperatures and sea ice are prescribed with 2010s or 2090s decadal averages from three ensemble members of transient RCP8.5 simulations from CM3. Anthropogenic pollutant emissions are constant from year to year throughout each simulation, fixed at 2010 or 2090 levels. Soil NO emissions are prescribed and constant from year to year (Naik *et al* 2013). Isoprene emissions are calculated online with a version of MEGAN (Guenther *et al* 2006, Emmons *et al* 2010, Rasmussen *et al* 2012). Lightning NO emissions are also calculated interactively; global lightning NO emissions scale with global surface temperature (John *et al* 2012).

Central to the land-atmosphere exchanges of water, energy, and reactive trace gases in AM3DD is the stomatal resistance ( $R_s$ ) simulated by LM3 (note that a resistance is the inverse of a conductance). The prognostic variable  $R_s$  for water vapor ( $\text{m s}^{-1}$ ) is calculated from net photosynthesis ( $A_{\text{net}}$ ) via the Leuning (1995) model:

$$R_s = \frac{1}{\text{LAI}} \frac{p_s}{RT_{\text{leaf}}} \frac{\left(1 + \frac{d_s}{d_0}\right) c_i - \Gamma}{m A_{\text{net}}} \quad (1)$$

The parameter  $R$  is the universal gas constant ( $\text{J mol air}^{-1} \text{K}^{-1}$ );  $T_{\text{leaf}}$  is leaf temperature (K);  $p_s$  is surface pressure (Pa);  $m$  is an empirical constant (unitless);  $d_s$  is the vapor pressure deficit ( $\text{kg H}_2\text{O kg air}^{-1}$ );  $d_0$  is an empirical constant ( $\text{kg H}_2\text{O}$

$\text{kg air}^{-1}$ );  $c_i$  is carbon dioxide concentration internal to the leaf ( $\text{mol CO}_2 \text{mol air}^{-1}$ );  $\Gamma$  is carbon dioxide compensation point of assimilation in the presence of dark respiration ( $\text{mol CO}_2 \text{mol air}^{-1}$ ); LAI is leaf area index ( $\text{m}^2 \text{m}^{-2}$ ).  $A_{\text{net}}$  ( $\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ ) is calculated following Farquhar *et al* (1980) and Collatz *et al* (1991, 1992).  $A_{\text{net}}$  is only calculated when LAI and photosynthetically active radiation at the canopy top are greater than zero.

The variable  $g_s$  is scaled by a fractional parameter that balances the water supply from the roots with demand when supply is less than demand (Milly *et al* 2014). The minimum value of  $g_s$  is  $0.01 \text{ mol m}^{-2} \text{s}^{-1}$ , and the maximum is  $0.25 \text{ mol m}^{-2} \text{s}^{-1}$  (both applied before conversion to  $\text{m s}^{-1}$ ).  $g_s$  of ozone is estimated by scaling  $g_s$  by the ratio of the diffusivity of ozone by the diffusivity of water vapor.

CUO requires concurrent estimates of the effective stomatal conductance ( $eg_s$ ) and ambient ozone concentrations.  $eg_s$  is the contribution of stomatal uptake to the ozone deposition velocity ( $v_d$ ), a measure of the efficiency of the total ozone depositional sink irrespective of surface ozone concentration, in velocity units. Hereinafter, we will use the term  $g_s$  to represent the conductance for ozone diffusion through stomata, whereas  $eg_s$  to represent the strength of the removal of ozone by stomata. The variable  $v_d$  ( $\text{m s}^{-1}$ ) is given by equation (2) in the dry deposition parameterization in AM3DD:

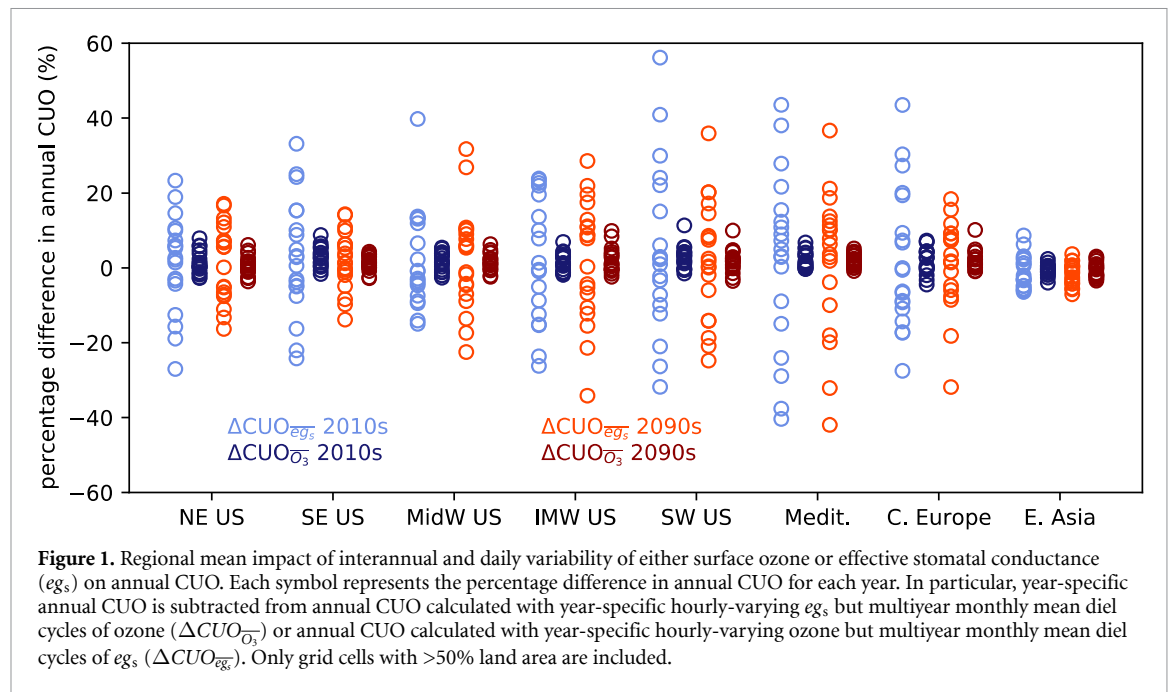
$$v_d = \left( R_a + \frac{1}{\frac{1}{R_{b,\text{veg}}} + \frac{1}{\frac{1}{R_s + R_m} + \frac{1}{R_{\text{cut}}}}} + \frac{1}{\frac{1}{R_{b,\text{veg}} + R_{\text{stem}}} + \frac{1}{R_{\text{ac}} + R_{b,\text{soil}} + R_{\text{soil}}}} \right)^{-1} \quad (2)$$

This parameterization is based on a resistance network analogous to the treatment of resistances in Ohm's law for electrical circuits. The variable  $R_a$  is the resistance to turbulent transport of ozone from the bottom of the atmospheric model to canopy height. In our big-leaf parameterization, all leaves are at canopy height. The variable  $R_{b,\text{veg}}$  is the resistance to transport through the quasi-laminar boundary layer around vegetation,  $R_m$  is the resistance to ozone reactions inside the leaf,  $R_{\text{cut}}$  is the resistance to ozone uptake by leaf cuticles,  $R_{\text{stem}}$  is the resistance to ozone uptake by stems,  $R_{\text{ac}}$  is the resistance to turbulent transport through the canopy to the soil,  $R_{b,\text{soil}}$  is the resistance to transport through the quasi-laminar boundary layer around soil, and  $R_{\text{soil}}$  is the resistance to ozone

uptake by soil. Descriptions of  $R_m$ ,  $R_{\text{cut}}$ ,  $R_{b,\text{veg}}$ ,  $R_{\text{stem}}$ ,  $R_{\text{ac}}$ , and  $R_{b,\text{soil}}$  can be found in Clifton *et al* (2020b).

CUO ( $\text{mmol O}_3 \text{m}^{-2}$ ) should be estimated at a frequency that captures surface ozone and  $eg_s$  diel cycles. We calculate CUO for the 2010s and 2090s as the cumulative sum of hourly stomatal ozone fluxes ( $F_{\text{stom},\text{O}_3}$ ;  $\text{mmol m}^{-2} \text{h}^{-1}$ ) over a year.  $F_{\text{stom},\text{O}_3}$  is calculated by multiplying hourly fields of ozone in  $\text{mmol m}^{-3}$  and  $eg_s$  in  $\text{m h}^{-1}$ .  $F_{\text{stom},\text{O}_3}$  follows Fick's law and assumes no ozone internal to the leaf given ozone's high reactivity with internal fluids and tissues (Laisk *et al* 1989, Wang *et al* 1995, Omasa *et al* 2000, Sun *et al* 2016).

We do not employ a detoxification threshold for ozone damage here. A threshold is primarily used to



account for the plant's ability to detoxify ozone after it enters stomata and pertains more to the estimation of plant damage from CUO than the amount of ozone actually entering the leaf. The focus of our paper is not to quantify plant damage, but instead to quantify how variability in  $eg_s$  and ambient ozone concentrations affect CUO.

We quantify the influence of daily and interannual variations in surface ozone versus  $eg_s$  on CUO by calculating CUO from hourly archived fields of  $eg_s$  and ozone from AM3DD (Clifton 2020). We identify the impact of variations in ozone on CUO by subtracting year-specific annual CUO from annual CUO calculated with year-specific hourly-varying  $eg_s$  but multiyear monthly mean diel cycles of ozone. In other words, for each year ( $y$ ), the difference in

annual CUO is:  $\Delta CUO_{O_3}(y) = \sum_{h=1}^{8760} \overline{O_3}(h) eg_s(y, h) -$

$\sum_{h=1}^{8760} O_3(y, h) eg_s(y, h)$  where the overbar is the multi-

year monthly mean diel cycle transposed into an hourly array for all hours in a year, and  $h$  is hour. To identify the impact of variations in  $eg_s$  on

CUO, we subtract year-specific annual CUO from annual CUO calculated with year-specific hourly-varying ozone but multiyear monthly mean diel

cycles of  $eg_s$  ( $\Delta CUO_{eg_s}(y) = \sum_{h=1}^{8760} O_3(y, h) \overline{eg_s}(h) -$

$\sum_{h=1}^{8760} O_3(y, h) eg_s(y, h)$ ).

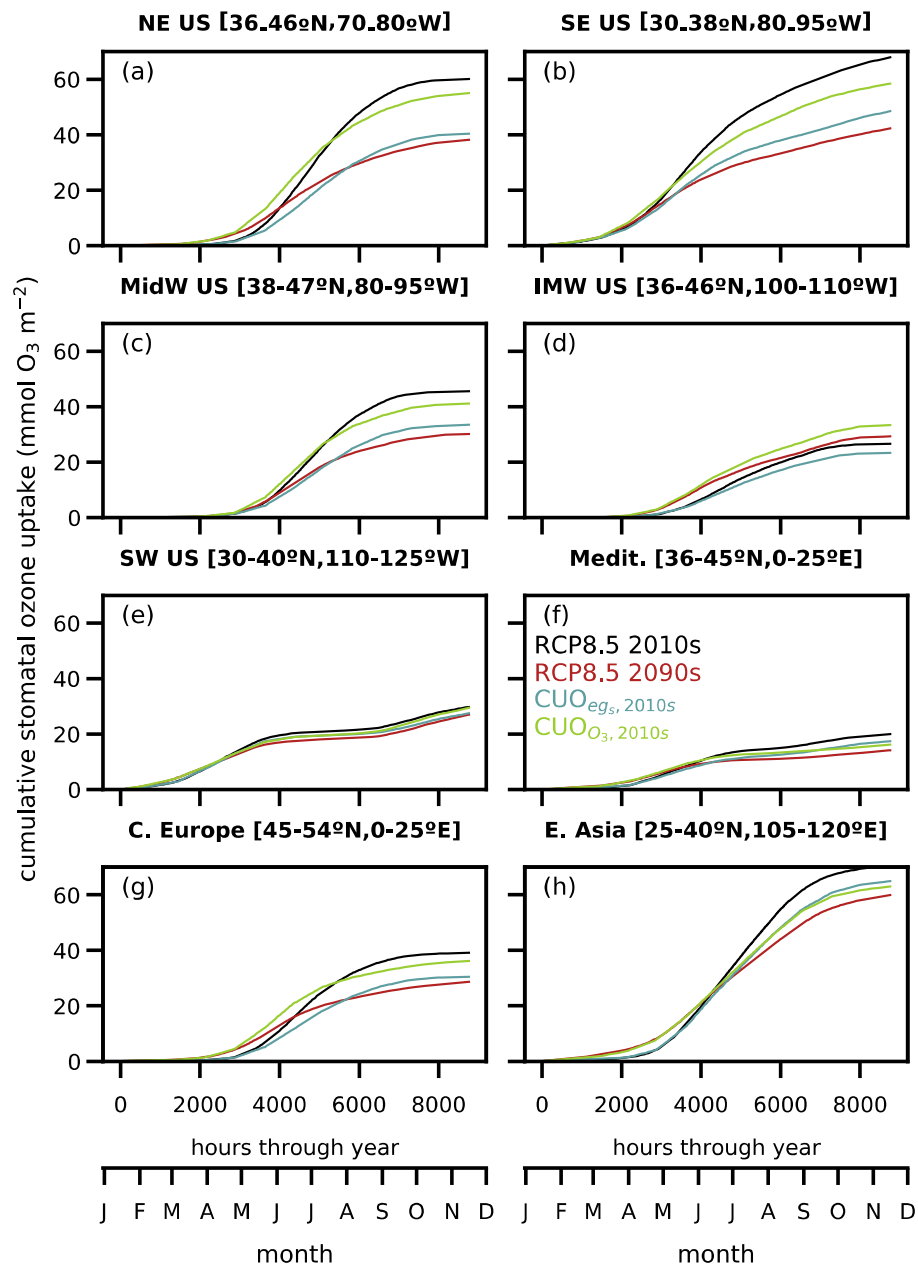
To identify how changes in  $eg_s$  versus surface ozone alter CUO over the 21st century, we calculate CUO in two ways: (i) with multiyear monthly mean diel cycles of ozone from the 2010s, but multiyear monthly mean diel cycles of  $eg_s$  from the 2090s ( $CUO_{O_3,2010}$ ) and (ii) with multiyear monthly

mean diel cycles of  $eg_s$  from the 2010s, but multi-year monthly mean diel cycles of ozone from the 2090s ( $CUO_{eg_s,2010}$ ). Inferring the role of changes in  $eg_s$  versus ozone with our offline calculation fails for any grid cell where  $eg_s$  is zero during the 2010s but nonzero at the end of the century. This happens for <1.4% of the grid-cell-hours for most regions examined (except 3.3% of the grid-cell-hours in the Midwest US and 4.2% in east Asia). However, we find that  $eg_s$  values that are nonzero at the 2090s but zero at the 2010s are too small or infrequent to impact CUO.

### 3. Large role for interannual variability in stomatal uptake on CUO

CUO varies strongly from year to year, with the 2010s annual CUO relative interannual spread (coefficient of variation) ranging from 3.7% to 21.4% across regions. Meteorological variability influences both surface ozone and  $g_s$ . For example, there is a strong correlation between ozone and temperature on daily and interannual timescales largely from the influence of transport patterns (Vukovich 1995, Barnes and Fiore 2013, Porter and Heald 2019, Kerr *et al* 2019). Variations in ecosystem-scale evapotranspiration and gross primary productivity, observable quantities related to  $g_s$ , are influenced by meteorology on hourly-to-interannual timescales and by phenology and soil moisture, which vary more slowly, on seasonal and interannual timescales (Wilson and Baldocchi 2000, Katul *et al* 2001, Stoy *et al* 2005, Chen *et al* 2009, Baldocchi *et al* 2018).

The influence of interannual variations in  $eg_s$  on annual CUO is substantially larger than the influence of interannual variations in surface ozone for most



**Figure 2.** Regional multiyear mean yearly progression of CUO for the 2010s, 2090s, and sensitivity calculations.  $CUO_{eg_s,2010}$  is calculated with 2010s multiyear monthly mean diel cycles of effective stomatal conductance, but 2090s multiyear monthly mean diel cycles of ozone while  $CUO_{O_3,2010}$  is calculated with 2090s multiyear monthly mean diel cycles of effective stomatal conductance, but 2010s multiyear monthly mean diel cycles of ozone. Only grid cells with >50% land area are included.

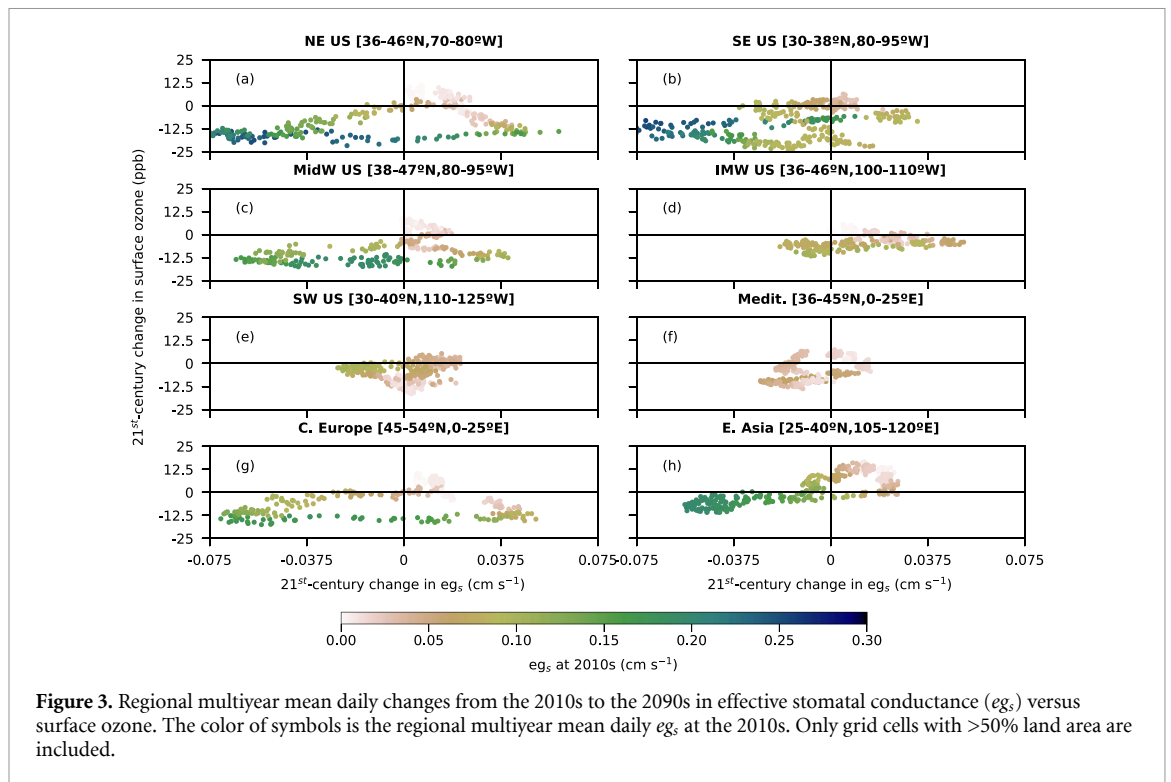
regions (figure 1). Variations in  $eg_s$  are critical for a given year's CUO relative to variations in ozone. Neglecting the role of  $eg_s$  variations yields over- or underestimates in annual CUO by up to 6%–58% across regions.

Only in east Asia is there a comparatively large role for variability in surface ozone. The relative interannual spread in annual  $eg_s$  in east Asia is weak relative to the other regions (4.1% versus 11.3%–22.8%) while the relative interannual spread in annual ozone is more within the range of other regions (1.4% versus 1.4%–2.6%) at the 2010s, suggesting that low  $eg_s$  variability leads to the larger relative role for ozone variability there. Low  $eg_s$  variability follows little

hydroclimate variability—east Asia has high simulated summer rainfall and low relative interannual variation in rainfall relative to other regions.

While  $eg_s$  interannual and daily variability is still more important for CUO than surface ozone interannual and daily variability at the 2090s, the absolute impact of  $eg_s$  variability lessens for several regions at the 2090s (figure 1). The smaller role of  $eg_s$  variability at the 2090s may be due to stomatal closure under high carbon dioxide and thus a weaker plant sensitivity to environmental stress such as drought (e.g. Field *et al* 1995, Swann *et al* 2016). Indeed, the model projects increases in regional summer mean water use efficiency (gross primary productivity divided





by transpiration) of 40%–100% depending on the region.

#### 4. Twenty-first century changes in CUO under RCP8.5

Figure 2 shows the progression of CUO throughout the year at the 2010s and 2090s. CUO increases earlier in the year by the 2090s for all regions in our analysis. However, the 21st century change in the magnitude and sign of CUO by the end of the year varies by region, with annual decreases from the 2010s to the 2090s in CUO ranging from 2 to 24  $\text{mmol O}_3 \text{ m}^{-2}$ . Annual increases in CUO only happen in the IMW US (3  $\text{mmol O}_3 \text{ m}^{-2}$ ).

Comparing 2010s and 2090s CUO with  $CUO_{O_3,2010}$  and  $CUO_{eg_s,2010}$  shows  $eg_s$  drives the earlier CUO increase at the 2090s (figure 2). Earlier leaf out or higher year-round LAI at the 2090s lead to higher springtime  $eg_s$  (figures S2 and S3) (available online at [stacks.iop.org/ERL/15/114059/mmedia](https://stacks.iop.org/ERL/15/114059/mmedia)) and thus higher springtime CUO. Rising temperatures lead to earlier leaf out (e.g. Badeck *et al* 2004, Richardson *et al* 2013, Melaas *et al* 2018) and the long-term effects of carbon dioxide fertilization lead to higher LAI (e.g. Los *et al*, 2013, Zhu *et al* 2016, Mao *et al* 2016).

There are substantial 21st century increases in winter and sometimes early spring surface ozone under RCP8.5 over the northeast US, Midwest US, central Europe, and east Asia in our simulations (figure S1) (Clifton *et al* 2020b). These

ozone increases tend to occur at times with low  $eg_s$  (figure 3), and thus do not substantially impact CUO. Increases in winter and early spring surface ozone follow regional reductions in anthropogenic  $\text{NO}_x$  under RCP8.5 in  $\text{NO}_x$ -saturated regions of the northern midlatitudes (Clifton *et al* 2014). This winter/early spring ozone increase is amplified by a doubling of methane under RCP8.5 (Clifton *et al* 2014). Increased stratosphere-to-troposphere ozone exchange over northern midlatitudes with climate change and stratospheric ozone recovery (Hegglin and Shepherd 2009, Kawase *et al* 2011, Banerjee *et al* 2016) may also contribute to higher spring surface ozone in regions like the IMW US (e.g. Fiore *et al* 2015).

Large decreases in annual CUO tend to occur in regions with large decreases in summer surface ozone (compare figures 2 and S1). Summer ozone decreases under RCP8.5 from the 2010s to the 2090s in all of the regions examined here (figure S1). Decreases in summer surface ozone follow regional reductions in anthropogenic  $\text{NO}_x$  emissions under RCP8.5 (Gao *et al* 2013, Pfister *et al* 2014, Clifton *et al* 2014, Rieder *et al* 2018), which are 66%–69% for 2010 to 2090 for the regions considered. The 21st century summer surface ozone decreases range from  $-7$  ppb (east Asia) to  $-18$  ppb (southeast US) (figure S3) (Clifton *et al* 2020b). Differences in 2010 regional  $\text{NO}_x$  emissions, local ambient chemistry, and dry deposition, as well as background ozone contribute to regionally varying responses to changes in regional  $\text{NO}_x$  emissions.

While springtime CUO is higher for all regions by the 2090s, summertime CUO is lower for many regions because summertime  $eg_s$  is lower by the 2090s (figures 2 and S3). Lower summertime CUO from changes in  $eg_s$  counteracts higher springtime CUO from changes in  $eg_s$  for all regions except the IMW and southwest US (compare 2010s and ozone\_2010s CUO in figure 2). Similar summertime  $eg_s$  at the 2010s and 2090s in the IMW and southwest US (figure S3) is likely due to offsetting between the expansion of vegetation coverage in these regions (Clifton *et al* 2020b) and the short-term impacts of high carbon dioxide on  $eg_s$  (i.e. stomatal closure) (e.g. Field *et al* 1995, Betts *et al* 1997, Ainsworth and Rogers 2007). Lower 2090s summer  $eg_s$  in the other regions (figure S3) likely follows stomatal closure due to high carbon dioxide.

The 21st century  $eg_s$  changes sometimes counteract or amplify the influence of surface ozone changes on CUO (figure 2). For the IMW US, slightly higher  $eg_s$  for most of the year increases CUO and lower ozone decreases CUO, yielding little 21st century CUO change by the end of the year. For most other regions, lower  $eg_s$  during nonwinter months (figure S3) leads to larger reductions in annual CUO by the 2090s, relative to the CUO reductions due to changes in ozone alone. For the SW US, reductions in annual CUO mostly stem from ozone reductions. While offsetting by temporally opposing changes in  $eg_s$  and/or ozone imply that 21st century changes in annual CUO in some regions may be relatively small, temporal differences in the plant sensitivity to ozone (e.g. Musselman *et al* 2006, Heath *et al* 2009) may need to be considered in assessing how these CUO changes affect ecosystems.

In general, 21st century changes in  $eg_s$  are uncertain, especially with respect to the impacts of increasing carbon dioxide and how other processes may offset or amplify such impacts (Friedlingstein *et al* 2006, Wieder *et al* 2015, Terrer *et al* 2016, Smith *et al*, 2016, 2016b, Alton 2018, Humphrey *et al* 2018, Green *et al* 2019, Sulman *et al* 2019, Yuan *et al* 2019). This uncertainty implies a need to explore simulated responses of CUO to 21st century changes across different land models and individual model configurations, as well as theoretical frameworks for stomatal functioning (Katul *et al* 2010, Medlyn *et al* 2011, Wang *et al* 2017, 2020).

## 5. Conclusion

Here we probe the cumulative ozone uptake by stomata, a metric that accounts for the amount of ozone entering the leaf that can cause physiological injury. We examine the relative importance of temporal changes in surface ozone versus stomatal uptake using a new version of the GFDL global earth system model where the atmosphere and land are coupled through exchanges of carbon, water, and energy as well as

dry deposition of reactive gases including ozone. We find that accurate estimates of the cumulative stomatal ozone uptake require considering interannual variations in stomatal functioning, supporting observational and modeling evidence that recent changes in cumulative stomatal ozone uptake cannot be explained by ozone changes alone (e.g. Anav *et al* 2019, Ronan *et al* 2020). We emphasize that our study is a sensitivity analysis of the influence of ozone versus stomatal conductance on the cumulative stomatal ozone uptake—an assessment of changes in ozone damage requires advanced understanding of plant detoxification ability and responses to ozone at regional scales. Decreases in water use efficiency from ozone plant damage (Lombardozzi *et al* 2015, Hoshika *et al* 2015) may increase the effect of water stress on plants and thus alter interannual variability in stomatal activity, implying a need to better understand how variability in stomatal ozone uptake feeds back on itself. Nonetheless, our results suggest that, without substantial changes in  $NO_x$  emissions from year to year, the highest ozone damage may occur in highly productive (i.e. high stomatal conductance) years, rather than high-ozone years. The important role for interannual variability and 21st century changes in stomatal conductance highlighted here challenges the validity of widely used approaches employing only ambient ozone concentrations to assess ozone plant damage and protect vegetation.

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## Data availability statement

The data that support the findings of this study are openly available at the following DOI: <https://doi.org/10.5065/wkdj-2s62>

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