



Implementation of trait-based ozone plant sensitivity in the Yale Interactive terrestrial Biosphere model v1.0 to assess global vegetation damage

4

5 Yimian Ma^{1, 2}, Xu Yue^{3*}, Stephen Sitch^{4*}, Nadine Unger³, Johan Uddling⁵, Lina M. Mercado^{4, 6},

6 Cheng Gong⁷, Zhaozhong Feng⁸, Huiyi Yang⁹, Hao Zhou^{1, 2}, Chenguang Tian^{1, 2}, Yang Cao^{1, 2},

7 Yadong Lei¹⁰, Alexander W. Cheesman^{4,11}, Yansen Xu⁸, Maria Carolina Duran Rojas¹²

- 8 9
- ¹⁰ ¹ Climate Change Research Center, Institute of Atmospheric Physics, Chinese Academy of Sciences,
- 11 Beijing, 100029, China
- ¹² ² University of Chinese Academy of Sciences, Beijing, 100029, China
- 13 ³ Jiangsu Key Laboratory of Atmospheric Environment Monitoring and Pollution Control, Jiangsu
- 14 Collaborative Innovation Center of Atmospheric Environment and Equipment Technology, School of
- 15 Environmental Science and Engineering, Nanjing University of Information Science and Technology,
- 16 Nanjing, 210044, China
- ⁴ Faculty of Environment, Science and Economy, University of Exeter, Exeter, EX4 4RJ, UK
- ¹⁸ ⁵ Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, P.O.
- 19 Box 461, 40530, Sweden
- ⁶ UK Centre for Ecology and Hydrology, Benson Lane, Wallingford, OX10 8BB, UK
- ²¹ State Key Laboratory of Atmospheric Boundary Layer Physics and Atmospheric Chemistry (LAPC),
- 22 Institute of Atmospheric Physics, Chinese Academy of Sciences, Beijing, 100029, China
- ⁸ School of Applied Meteorology, Nanjing University of Information Science and Technology, Nanjing,
 210044, China
- ⁹ Livelihoods and Institutions Department, Natural Resources Institute, University of Greenwich, Kent,
 ME4 4TB, UK
- ²⁷ ¹⁰ Chinese Academy of Meteorological Sciences, Beijing, 100081, China
- ¹¹ Centre for Tropical Environmental and Sustainability Science, College of Science & Engineering,
 James Cook University, Cairns, Queensland, 4870 Australia
- ¹² College of Engineering, Mathematics, and Physical Sciences, University of Exeter, EX4 4PY,
 UK
- 31 32
- 33 *Correspondence to*: Xu Yue (<u>yuexu@nuist.edu.cn</u>) and Stephen Sitch (<u>S.A.Sitch@exeter.ac.uk</u>)
- 34
- 35





36

37

38

Abstract

A major limitation in modeling global ozone (O_3) vegetation damage has long been the reliance on 39 empirical O₃ sensitivity parameters derived from a limited number of species and applied at the level of 40 plant functional types (PFTs), which ignore the large interspecific variations within the same PFT. Here, 41 we present a major advance in large-scale assessments of O₃ plant injury by linking the trait leaf mass per 42 area (LMA) and plant O₃ sensitivity in a broad and global perspective. Application of the new approach 43 and a global LMA map in a dynamic global vegetation model reasonably represents the observed 44 interspecific responses to O₃ with a unified sensitivity parameter for all plant species. Simulations suggest 45 a contemporary global mean reduction of 4.8% in gross primary productivity by O₃, with a range of 1.1%-46 12.6% for varied PFTs. Hotspots with damages > 10% are found in agricultural areas in the eastern U.S., 47 western Europe, eastern China, and India, accompanied by moderate to high levels of surface O₃. 48 Furthermore, we simulate the distribution of plant sensitivity to O₃, which is highly linked with the 49 inherent leaf trait trade-off strategies of plants, revealing high risks for fast-growing species with low 50 LMA, such as crops, grasses and deciduous trees. 51





53 **1. Introduction**

Tropospheric ozone (O_3) has long been recognized as a hazardous pollutant for plants (Reich and 54 Amundson, 1985; Richards et al., 1958). As a strong oxidant, O₃ can cause damage to leaf cells and 55 modulate the carbon balance of ecosystems through both direct and indirect impacts on plant function 56 (Ainsworth et al., 2012; Feng et al., 2014; Wittig et al., 2009). To date, O₃ fumigation experiments have 57 revealed a large variation in O₃ sensitivities among and within plant functional types (PFTs) (Buker et al., 58 2015; Mills et al., 2018a) (Table S1). Generally, needleleaf trees, deciduous woody plants, and crop 59 species show ascending sensitivities to O₃ (Buker et al., 2015; Davison and Barnes, 1998; Reich and 60 Amundson, 1985). The cause of such variation is not fully understood and thus has not been uniformly 61 described in vegetation models (Massman et al., 2000; Tiwari et al., 2016). As a result, large-scale 62 assessments of O₃ vegetation damage have to rely on a PFT-based range of sensitivity parameters derived 63 from a limited number of plant species (Felzer et al., 2009; Lombardozzi et al., 2015; Sitch et al., 2007). 64 For example, Sitch et al. (2007) (hereafter S2007) attempted to envelop the range of O₃ impacts by 65 assuming all species within a PFT are either "high" or "low" sensitive to O₃, which cannot resolve intra-66 PFT variations and thus may cause large uncertainties in regional to global assessments. 67

68

Recent observations revealed a uniform plant sensitivity to O₃ if stomatal O₃ flux is expressed based on 69 leaf mass rather than leaf area (Feng et al., 2018; Li et al., 2016; Li et al., 2022). The trait of leaf mass per 70 area (LMA) is an important metric linking leaf area to mass. In a comparative study with 21 woody 71 species (Li et al., 2016) and a meta-analysis of available experimental data (Feng et al., 2018), the dose-72 response relationship (DRR) shows convergent O₃ sensitivities for conifer and broadleaf trees if the area-73 based stomatal uptake was converted to the mass-based flux with LMA. Meanwhile, a large number of 74 trait observations were synthesized by global networks in recent decades (Gallagher et al., 2020). The 75 TRY initiative (Kattge et al., 2011) is one of the most influential datasets with 2.3 billion trait data by the 76 year 2021. Based on the TRY dataset, global LMA was estimated with upscaling techniques such as 77 Bayesian modeling (Butler et al., 2017) (thereafter B2017) or the random forest model (Moreno-Martinez 78 79 et al., 2018) (thereafter M2018). These advances in the retrieval of LMA provide the possibility to depict more accurate O₃ vegetation damage at the global scale. 80





81

Here, we present a major advance in large-scale assessments of O₃ plant damage using a trait-based 82 approach. We implement LMA into a stomatal flux-based O_3 damage framework aiming at a unified 83 representation of plant O₃ sensitivities over the global grids. We couple this new approach to the Yale 84 Interactive terrestrial Biosphere (YIBs) model (Yue and Unger, 2015) and evaluate the derived O₃ 85 sensitivities against observations. We further assess contemporary O₃ impacts on global gross primary 86 productivity (GPP) in combination with the recently developed LMA datasets (Butler et al., 2017; 87 Gallagher et al., 2020; Moreno-Martinez et al., 2018) (Fig. S1a) and the multi-model ensemble mean 88 surface O₃ concentrations (Fig. S1b). The updated risk map for O₃ vegetation damage is used to identify 89 the regions and species with the largest sensitivity to O₃ threats. 90

91

92 2. Scheme development and calibration

93 2.1 The trait-based O₃ vegetation damage scheme

We develop the new scheme based on the S2007 framework for transient O₃ damage calculation. In the original S2007 scheme, the undamaged fraction *F* for net photosynthetic rate is dependent on the excessive area-based stomatal O₃ flux, which is calculated as the difference between f_{O3} and PFT-specific area-based threshold *y*, and modulated by the sensitivity parameter a_{PFT} :

98
$$F = 1 - a_{PFT} \times max\{f_{03} - y, 0\}$$
 (1)

99 where a_{PFT} is calibrated and varies among PFTs with a typical range from "low" to "high" values 100 indicating uncertainties of plant species within the same PFT in Sitch et al. (2007). The stomatal O₃ flux 101 f_{O3} is calculated as:

102
$$f_{O3} = \frac{[O_3]}{r + \left[\frac{k_{O3}}{g_p \times F}\right]}$$
 (2)

where $[O_3]$ is the O₃ concentration at the reference level (nmol m⁻³), *r* is the aerodynamic and boundary layer resistance between leaf surface and reference level (s m⁻¹). k_{O3} setting to 1.67 represents the ratio of





leaf resistance for O₃ to that for water vapor. g_p represents potential stomata conductance for H₂O (m s⁻¹).

107

Studies suggested that LMA could be used to unify the area-based plant sensitivities to O_3 (Feng et al., 2018; Li et al., 2016), resulting in a constant mass-based parameter *a* independent of plant species and PFTs:

$$111 \quad a = a_{PFT} \times LMA \tag{3}$$

Here, we convert the area-based O_3 stomatal flux expression in Equation (1) to a mass-based flux as follows:

114
$$F = 1 - a \times \max\left\{\frac{f_{03}}{L_{MA}} - x, 0\right\}$$
 (4)

where the new sensitivity parameter *a* is a cross-species constant (nmol⁻¹ s g); *LMA* is leaf mass per area (g m⁻²); the flux threshold is replaced by a mass-based value of *x* (nmol g⁻¹ s⁻¹) (Feng et al., 2018). This equation is applied at the timestep of photosynthesis calculation in the YIBs model (i.e. hourly). The updated LMA-based framework (YIBs-LMA) reduces the number of O₃ sensitivity parameters from three for each PFT (Sitch et al., 2007) in S2007 to a single parameter *a* for all PFTs. For YIBs-LMA framework, the default value of the *x* threshold in Equation (4) is set to 0.019 nmol g⁻¹ s⁻¹ as recommended by Feng et al. (2018).

122

123 2.2 Dose-response relationship (DRR)

124 We compare the simulated and observed sensitivities to O₃ so as to calibrate the LMA-based scheme. In

125 field experiments, DRR is used to quantify species-specific damage by O₃ with a generic format as follows:

126
$$R = 100 + S_0 \times \phi_{03}$$
 (5)

where R (%) is the relative percentage of a bio-indicator (such as biomass or yield) after and before O₃ damage; ϕ_{O3} is an area-based O₃ metric (e.g., POD_y measured in sunlit leaves at the top of canopy); S_O (usually negative) is the observed sensitivity derived as the slope of linear relationship between R and

130 ϕ_{03} . We collected S₀ from DRRs with conventional criteria (typically POD_{v=1} for natural PFTs and

131 $POD_{y=6}$ for crops as dose metrics (CLRTAP, 2017); the bio-indicators include the relative biomass for

132 natural PFTs and relative yield for crops) among plant species from International Cooperative Programme





- 133 on Effects of Air Pollution on Natural Vegetation and Crops (CLRTAP) (CLRTAP, 2017) and multiple
- 134 literature sources (Table S1). Such observations are used to calibrate the LMA-based scheme.
- 135
- As a comparison with observations, we calculate annual relative GPP percentage (R_{GPP} , %) and POD_y of sunlit leaves in first canopy layer (mmol m⁻² year⁻¹, based on per leaf area) from the vegetation model to
- 138 derive the slopes (S_S) of simulated DRRs. Here, POD_v is a diagnostic variable calculated as:

139
$$POD_y = \int (f_{03} - y)$$
 (6)

where f_{O3} represents the stomatal O₃ flux under instant O₃ stimulus at each timestep, which can be calculated following Equation (2) on the leaf level; *y* is the prescribed critical level (1 nmol m⁻² s⁻¹ for natural or 6 nmol m⁻² s⁻¹ for crop species (CLRTAP, 2017)). Excessive O₃ flux above y is accumulated for the top canopy layer and over the growing season to derive the *POD_y*. Simulated *S_S* is calculated as the slope of regression between simulated *R_{GPP}* (%) and *POD_y* at the PFT level. Only the dominant PFT in each grid is considered for the estimate of *S_S* at both PFT-level or gridded analyses.

146

147 Similarly, mass-based POD_x is derived from O₃ impacted f_{O3} (nmol m⁻² s⁻¹) in Equation (2), together with 148 gridded LMA (g m⁻²) and mass-based threshold x (nmol g⁻¹ s⁻¹) as:

149
$$POD_x = \int \left(\frac{f_{03}}{LMA} - x\right)$$
(7)

150

151 2.3 Simulations and calibrations

We perform two groups of supporting experiments (Table 1). The first group explores modeling uncertainties associated with the mass-based framework: (1) YIBs-LMA_B2017 replaces the default LMA map of M2018 (Moreno-Martinez et al., 2018) with B2017 (Butler et al., 2017). (2) YIBs-LMA_PFT applies PFT-specific LMA values (Table S2) for each PFT without considering global LMA geo-gradient. (3) YIBs-LMA_T replaces the default threshold of *x*=0.019 nmol g⁻¹ s⁻¹ with *x* =0.006 nmol g⁻¹ s⁻¹, which is an alternative parameter suggested by observations (Feng et al., 2018). The second group of supporting experiments explores the differences between mass-based and S2007 area-based





frameworks. Typically, S2007 has a "low to high" a_{PFT} range for each PFT. Here, a mean sensitivity parameterization of S2007 (YIBs-S2007_adj) is re-calibrated according to S_O in Table S1.

161

For all supporting experiments, the parameter *a* for YIBs-LMA or the eight mean a_{PFT} for YIBs-S2007_adj are derived with the optimal 1:1 fitting between S_S and S_O to minimize the possible biases (Tables S3-S7). Since S_O are available only for six out of the eight YIBs PFTs, including EBF, NF, DBF, C₃ grass, C₄ grass, and crop (Table S1), S_O of these PFTs are used for calibration.

166

167 2.4 YIBs model and forcing data

In this study, all O₃ vegetation damage schemes are implemented in the YIBs model (Yue and Unger, 168 2015). The YIBs is a process-based dynamic global vegetation model incorporated with well-established 169 carbon, energy, and water interactive schemes. The model applies the same PFT classifications as the 170 Community Land Model (Bonan et al., 2003) (Fig. S2). Eight PFTs are employed including evergreen 171 broadleaf forest (EBF), needleleaf forest (NF), deciduous broadleaf forest (DBF), cold shrub (C SHR), 172 arid shrubland (A SHR), C₃ grassland (C3 GRA), C₄ grassland (C4 GRA), and cropland (CRO) (Fig. 173 S2). For each PFT, phenology is well-evaluated (Yue and Unger, 2015) to generate a reliable growing 174 season, which is crucial for the simulation of stomatal O₃ uptake (Anav et al., 2018). Photosynthesis and 175 stomatal processes are calculated using Farquhar et al. and Ball-Berry algorithms (Ball et al., 1987; 176 Farquhar et al., 1980), respectively. Leaf area index (LAI) and tree height are predicted dynamically based 177 on vegetation carbon allocation. The YIBs model has joined the multi-model ensemble project TRENDY 178 and showed reasonable performance in the simulations of global biomass, GPP, LAI, net ecosystem 179 exchange, and soil carbon relative to observations (Friedlingstein et al., 2020). Key plant biogeochemical 180 parameters of the YIBs model are adjusted for this research (Table S8). 181

182

183 The hourly modern-era retrospective analysis for research and applications version 2 (MERRA2) climate

184 reanalyses (Gelaro et al., 2017) are used to drive the YIBs model. The gridded LMA required for the main

185 mass-based simulation is derived from Moreno-Martinez et al. (2018) (M2018), which shows the highest

value of >150 g m⁻² for needleleaf forest at high latitudes while low values of \sim 40 g m⁻² for grassland and





187 cropland (Fig. S1a and Fig. S2). Grids with missing LMA data are filled with the mean of the 188 corresponding PFT. Contemporary O₃ concentration fields in the year of 2010 from the multi-model mean 189 in Task Force on Hemispheric Transport of Air Pollutants (TF-HTAP) experiments (Turnock et al., 2018) 190 (Fig. S1b) are used as forcing data. The original monthly O₃ data are downscaled to hourly using the 191 diurnal cycle predicted by the chemistry-climate-carbon fully coupled model ModelE2-YIBs (Yue and 192 Unger, 2015). All data are interpolated to the spatial resolution of $1^{\circ} \times 1^{\circ}$.

193

194 **3. Results**

195 **3.1 Comparison of simulated sensitivities with observations**

Simulated relative GPP percentage (R_{GPP}) at global grids were sorted by dominant PFTs (Fig. S2) and 196 plotted against area-based accumulated phytotoxic O_3 dose above a threshold y nmol m⁻² s⁻¹ (POD_{y=1}) at 197 the corresponding grids (Fig. 1). The DRR shows varied slopes among different PFTs, resulting in a 198 coefficient of determination (R²) around 0.54 for all PFTs (Figs 1a-1c). We further calculated the mass-199 based accumulated phytotoxic O₃ dose above a threshold of 0.019 nmol g s⁻¹ (POD_{x=0.019}) and compared 200 it with R_{GPP}. The updated DRR showed convergent slopes and reached a high R² of 0.77 across all PFTs 201 (Figs 1d-1f), suggesting that the mass-based scheme could better unify O_3 sensitivities among different 202 PFTs. 203

204

We then calibrated the single, best-fit a value for YIBs-LMA framework by minimizing the absolute 205 difference between simulated (S_S) and observed (S_O) slopes of O₃ DRR for all PFTs. With different a 206 parameters, the YIBs-LMA framework yielded considerably high R² of ~1.0 but varied biases between 207 simulated and observed O₃ impacts across PFTs (Fig. 2). Both the 1:1 fitting and the lowest bias between 208 S_S and S_O were achieved with an optimal a = 3.5 nmol⁻¹ s g (Fig. 2c). Consistent with observations, YIBs-209 LMA with this optimal a parameter simulated low S_S of -0.18% and -0.36% per mmol m⁻² year⁻¹ of POD_{y=1} 210 for evergreen broadleaf forest and needleleaf forest, respectively (Figs 3a, b), median S_{S} from -0.53% per 211 mmol m⁻² year⁻¹ for arid shrubland (Fig. 3e), and high S_S from -0.64% to -1.04% per mmol m⁻² year⁻¹ for 212 deciduous broadleaf forest, C_3/C_4 grassland, cropland and cold shrubland (-3.28% for crops with POD_{v=6}, 213 Figs 3c-d, 3f-h). 214





215

216 **3.2 Global map of O₃ vegetation damage**

We estimated contemporary GPP reductions induced by O₃ with the global concentrations of surface O₃ 217 (Fig. S1b) in the year of 2010. The YIBs-LMA framework using an increase of a parameter yielded an 218 almost linearly enhancement of global GPP reduction (Fig. S3) with consistent spatial distributions (Fig. 219 S4). The simulation with the optimal $a = 3.5 \text{ nmol}^{-1} \text{ s g predicted a global GPP reduction of 4.8% (Fig.$ 220 4a), which was similar to the value estimated with the area-based S2007 scheme (YIBs-S2007 adj, Table 221 1). Large reductions of >10% were predicted over eastern U.S., western Europe, eastern China, and India 222 (Fig. 4a). Hotspots were mainly located in cropland and agricultural areas mixed with deciduous broadleaf 223 forest or grassland, accompanied with moderate to high levels of surface O₃. Few discrepancies between 224 the damage maps of YIBs-LMA and YIBs-S007 adj were found (Fig. 4b), even though the number of 225 parameters was greatly reduced in YIBs-LMA scheme. 226

227

For YIBs-LMA, PFTs with low LMA such as cropland, grassland, and deciduous broadleaf forest account 228 for 73.3 Pg C yr⁻¹ (50.0%) of the global GPP (Table S9). However, these PFTs contributed to a total GPP 229 reduction of 5.4 Pg C yr⁻¹ (75.5% of total GPP loss) by O₃ damage. In contrast, evergreen broadleaf and 230 needleleaf forests with high LMA accounted for 48.8 Pg C yr⁻¹ (33.0%) of total GPP but yielded only a 231 reduction of 0.75 Pg C yr⁻¹ (10.5% of total GPP loss). Differences in GPP percentage losses were in part 232 associated with the global pattern of O3 concentrations, which were usually higher over mid-latitudes with 233 populated cities and dense crop plantations (Fig. S1b). However, the differences in LMA and simulated 234 O₃ sensitivities of these PFTs were the main cause of discrepancies in GPP damage at the large scale. 235

236

237 3.3 Uncertainties of the LMA-based scheme

We quantified the uncertainties of LMA-based shceme by comparing simulated GPP damages among different experiments (Table 1). The experiment with the alternative LMA map of B2017 (Fig. S5) showed a slightly enhanced GPP reduction of 5.3% (Fig. 5a) but similar spatial patterns compared with YIBs-LMA using M2018 (Fig. 4a). However, B2017 has a much less source of LMA data than M2018 (~40%), leading to some unexpected areas with high O₃ threats such as the tundra in Arctic region (Fig.





S6). The experiment with PFT-specific LMA estimated a global GPP reduction of 4.6% (Fig. 5b) with 243 consistent spatial pattern as the prediction with YIBs-LMA, suggesting the reasonable application of PFT-244 level LMA at the lack of global LMA data. The experiment with an alternative threshold flux (Feng et al., 245 2018) of 0.006 nmol g⁻¹ s⁻¹ estimated a higher GPP reduction of 6.5% by global O₃ (Fig. 5c) with 246 overestimations of O3 sensitivities for some tree PFTs (Fig. 6). The YIBs-S2007_adj run using 247 recalibrated PFT-level sensitivities predicts a similar global GPP damage of 4.8% as the YIBs-LMA run 248 with a high spatial correlation coefficient of 0.98 (Fig. 5d). All sensitivity experiments achieve consistent 249 results as the YIBs-LMA simulation with an uncertaintiv range from -0.2% to 1.7% and spatial correlation 250 coefficients larger than 0.94. 251

252

253 4. Discussion

254 4.1 Mechanisms behind the LMA-based approach

In recent decades, the plant science community examined how traits could be used to differentiate and 255 predict the functions of plant species (Reich et al., 1999; Reich et al., 1997). LMA, related to leaf density 256 and thickness, is a key trait reflecting many aspects of leaf function (Reich et al., 1998). In the field of O₃ 257 phytotoxicology, experiments have revealed plants with high LMA usually have thick leaves with 258 physical and chemical defenses (Poorter et al., 2009), which can strengthen their resistance to O₃ (Feng 259 et al., 2018; Li et al., 2016). On the contrary, plants with low LMA normally have thin leaves which are 260 likely to be less O₃-tolerant (Feng et al., 2018; Li et al., 2016). Moreover, it seems plausible that the 261 oxidative stress caused by a given amount of stomatal O₃ flux per unit leaf area would be distributed over 262 a larger leaf mass, and hence diluted, in a leaf with high LMA. Such a LMA-O₃ sensitivity relationship 263 can be well reproduced by our LMA-based model (Figs 7a and 7b). Below we explore the linkage between 264 O₃ plant sensitivities and the mutual adaptation of growth strategies and leaf morphology with plant leaf 265 trade-off theory (Reich et al., 1999; Shipley et al., 2006). 266

267

In the natural world, plants often adapt to maximize carbon uptake under prevailing conditions (Reich et al., 1998; Shipley et al., 2006). To make full use of resources in the growing season, leaves under varied living conditions choose either fast photosynthetic rates (fast-growing deciduous types) or long





photosynthesis duration (slow-growing evergreen types) with compatible leaf structures (Diaz et al., 2016; 271 Reich, 2014). The former species expand leaf area (low LMA) to maximize light interception while the 272 latter species produce thick and mechanically strong leaves (high LMA) with ample resistant substances 273 for durable utilization (Poorter et al., 2009) in resource-limited and/or environment-stressed habitats 274 (Wright et al., 2002). As a side effect of such leaf trade-offs, deciduous plants with their high rates of 275 photosynthesis, associated large stomatal conductance (Davison and Barnes, 1998; Henry et al., 2019), 276 and less total defense capacity through the leaf profile (Poorter et al., 2009), are highly O₃ sensitive 277 (Model in Fig. 8). In contrast, the moderate photosynthesis, relatively low maximum stomatal 278 conductance (Davison and Barnes, 1998; Henry et al., 2019), and reinforced dense leaves (Poorter et al., 279 2009) lead to low sensitivity for evergreen plants (Mode2 in Fig. 8). Therefore, in our modelling practice, 280 the mass-based O_3 gas exchange algorithm can be regarded as taking into account several interrelated 281 factors such as growth-driven gas exchange requirements, gas path length and biochemical reserves, in a 282 unified, simplified and effective manner via LMA. 283

284

285 4.2 Implication of potential risks for fast-growing plants

Our new approach reflected the general experimental findings that deciduous plants are much more 286 vulnerable to O₃ than evergreen species (Feng et al., 2018; Li et al., 2017), and in turn within a PFT, 287 early-successional/pioneers with low LMA are likely more vulnerable than late-successional/canopy trees 288 with high LMA (Fyllas et al., 2012). This law has been neglected in previous modeling studies due to the 289 dependence on the limited observed data used for PFT-specific tuning. Our LMA-based approach bridges 290 this gap through grid-based parameterization, and in addition, our data-model integration specifically 291 emphasizes the broad high risks for fast-growing plants, especially for crops. Among PFTs, crops may 292 endure the largest O₃ threats (Davison and Barnes, 1998; Feng et al., 2021; Mukherjee et al., 2021) 293 because they are artificially bred with high photosynthetic capacities (Richards, 2000), stomatal 294 conductance, generally low LMA (Bertin and Gary, 1998; Li et al., 2018; Wang and Shangguan, 2010; 295 Wu et al., 2018) (roughly 30-60 g m⁻²), and cultivated in populated regions with high ambient O₃ 296 297 concentrations. Modern technology aims to promote crop yield (Herdt, 2005), but this can potentially elevate crop sensitivities to O₃ (Biswas et al., 2013; Biswas et al., 2008). This study estimated the highest 298





annual mean GPP damage for crop, 12.6%, which is at the high end of the 4.4-12.4% of the O₃-induced 299 yield loss estimated for global modeling of soybean, wheat, rice, and maize (Mills et al., 2018b). 300 Furthermore, human-induced land use activities may also increase O₃ damage risks. The global demand 301 for food and commodities leads to the conversion of natural forests to irrigated croplands, grazing pastures, 302 and economical-tree plantations (Curtis et al., 2018; Zalles et al., 2021). Meanwhile, the urgent actions to 303 combat climate change promote large-scale afforestation and reforestation (Cook-Patton et al., 2020). 304 These land use changes with fast-growing plant species may increase the risks of terrestrial ecosystems 305 to surface O₃. 306

307

308 4.3 Advances in the global O₃ damage assessment

For the first time, we implemented plant trait LMA into a process-based O₃ impact modeling scheme and 309 obtained reasonable interspecific and inter-PFT O₃ responses supported by observations. This LMA-310 based approach indicates an important advance in global O_3 damage assessments. First, it significantly 311 reduces the number of required key parameters. To account for interspecific sensitivities, many schemes 312 have to define PFT-level parameters to cap the ranges of plant responses (Felzer et al., 2009; Lombardozzi 313 et al., 2015; Sitch et al., 2007). As a result, those schemes rely on dozens of parameters which increase 314 the uncertainties of modeling and the difficulties for model calibration. The LMA-based approach 315 requires the calibration of one single parameter a, largely facilitating its application across different 316 vegetation models. Second, the new approach accounts for the continuous spectrum of O₃ sensitivities. 317 Previous studies usually categorized species into groups of low or high O₃ sensitivity, depending on very 318 limited data from O₃ exposure experiments. As a result, gridcells for a specific PFT share the same 319 sensitivities regardless of their geographic locations and ecosystem characteristics. In reality, there are 320 hundreds and thousands of plant species in each PFT and they usually have large variation in biophysical 321 parameters including LMA and O₃ sensitivities. The LMA-based approach takes advantage of the newly 322 revealed unifying concept in O₃ sensitivity (Feng et al., 2018; Li et al., 2016; Li et al., 2022) and the 323 recent development in a trait-based LMA global map (Fig. S1a). Such configurations present a spectrum 324 325 of gridded O₃ sensitivities (Fig. 7a) following the variations of LMA and bring the possibility of capturing spatiotemporal variation in vegetation O_3 sensitivity through time-sensitive LMA products in the future. 326





327

328 Code availability

329 The codes of YIBs model with LMA-based O₃ damaging scheme are shared at 330 <u>https://zenodo.org/record/6348731</u>.

331

332 Data availability

Results of all simulations (listed in Table 1) are available upon request. Data for Figures in the main article are shared at https://zenodo.org/record/6348731. The global maps of specific leaf area (SLA) to derive LMA for M2018 and B2017 are from https://www.try-db.org/TryWeb/Data.php#59 and https://github.com/abhirupdatta/global_maps_of_plant_traits, respectively. Monthly O₃ data is from https://doi.org/10.5194/acp-18-8953-2018. Calibration data are summarized in Table S1.

338

339 Author Contributions

340 X.Y., S.S. and N.U. designed the research, Y.M.M. performed modeling, data analyses, virtualization and

341 wrote the draft. J.U, L.M., Z.Z.F, and A.W.C advised on concepts and methods. C.G. helped write draft.

342 H.Y.Y., M.C.D.R helped with coding. H.Z., C.G.T., Y.C., Y.D.L., and Y.S.X. helped with data collection.

343 All authors commented and revised the manuscript.

344

345 Competing interests

346 The authors declare no conflict of interests.

347

348 Financial support

Xu Yue acknowledges funding support from Jiangsu Science Fund for Distinguished Young Scholars
(grant no. BK20200040). Yimian Ma acknowledges financial support from China Scholarship Council
(CSC no. 201804910712). Johan Uddling acknowledges the strategic research area Biodiversity and
Ecosystems in a Changing Climate, BECC. SS, NU, LM, AC were supported by NERC funding
(NE/R001812/1).





355 References

- 356 Ainsworth, E. A., Yendrek, C. R., Sitch, S., Collins, W. J., and Emberson, L. D.: The Effects of Tropospheric Ozone on Net Primary 357 Productivity and Implications for Climate Change, Annu Rev Plant Biol, 63, 637-661, 2012.
- 358 Anav, A., Liu, Q., De Marco, A., Proietti, C., Savi, F., Paoletti, E., and Piao, S.: The role of plant phenology in stomatal ozone flux modeling, 359 Global Change Biol, 24, 235-248, 2018.
- 360 Ball, J. T., Woodrow, I. E., and Berry, J. A.: A model predicting stomatal conductance and its contribution to the control of photosynthesis
- 361 under different environmental conditions, Progress in Photosynthesis Research: Viith International Congress on Photosynthesis, doi: 362 10.1007/978-94-017-0519-6 48, 1987. 1987.
- 363 Bertin, N. and Gary, C.: Short and long term fluctuations of the leaf mass per area of tomato plants - Implications for growth models, Ann 364 Bot-London, 82, 71-81, 1998.
- 365 Biswas, D. K., Xu, H., Li, Y. G., Ma, B. L., and Jiang, G. M.: Modification of photosynthesis and growth responses to elevated CO2 by 366 ozone in two cultivars of winter wheat with different years of release, J Exp Bot, 64, 1485-1496, 2013.
- 367 Biswas, D. K., Xu, H., Li, Y. G., Sun, J. Z., Wang, X. Z., Han, X. G., and Jiang, G. M.: Genotypic differences in leaf biochemical, 368 physiological and growth responses to ozone in 20 winter wheat cultivars released over the past 60 years, Global Change Biol, 14, 46-59, 369 2008.
- 370 Bonan, G. B., Levis, S., Sitch, S., Vertenstein, M., and Oleson, K. W.: A dynamic global vegetation model for use with climate models: 371 concepts and description of simulated vegetation dynamics, Global Change Biol, 9, 1543-1566, 2003.
- 372 Buker, P., Feng, Z., Uddling, J., Briolat, A., Alonso, R., Braun, S., Elvira, S., Gerosa, G., Karlsson, P. E., Le Thiec, D., Marzuoli, R., Mills,
- 373 G., Oksanen, E., Wieser, G., Wilkinson, M., and Emberson, L. D.: New flux based dose-response relationships for ozone for European forest 374 tree species, Environ. Pollut., 206, 163-174, 2015.
- 375 Butler, E. E., Datta, A., Flores-Moreno, H., Chen, M., Wythers, K. R., Fazayeli, F., Banerjee, A., Atkin, O. K., Kattge, J., Amiaud, B., 376 Blonder, B., Boenisch, G., Bond-Lamberty, B., Brown, K. A., Byun, C., Campetella, G., Cerabolini, B. E. L., Cornelissen, J. H. C., Craine,
- 377 J. M., Craven, D., de Vries, F. T., Diaz, S., Domingues, T. F., Forey, E., Gonzalez-Melo, A., Gross, N., Han, W., Hattingh, W. N., Hickler,
- 378 T., Jansen, S., Kramer, K., Kraft, N. J. B., Kurokawa, H., Laughlin, D. C., Meir, P., Minden, V., Niinemets, U., Onoda, Y., Penuelas, J.,
- 379 Read, Q., Sack, L., Schamp, B., Soudzilovskaia, N. A., Spasojevic, M. J., Sosinski, E., Thornton, P. E., Valladares, F., van Bodegom, P. M.,
- 380 Williams, M., Wirth, C., and Reich, P. B.: Mapping local and global variability in plant trait distributions, Proc Natl Acad Sci U S A, 114,
- 381 E10937-E10946, 2017.
- 382 CLRTAP: The UNECE Convention on Long-range Transboundary Air Pollution, Manual on Methodologies and Criteria for Modelling and 383 Mapping Critical Loads and Levels and Air Pollution Effects, Risks and Trends: Chapter III Mapping Critical Levels for Vegetation, 2017.
- 384 2017.
- 385 Cook-Patton, S. C., Leavitt, S. M., Gibbs, D., Harris, N. L., Lister, K., Anderson-Teixeira, K. J., Briggs, R. D., Chazdon, R. L., Crowther, 386 T. W., Ellis, P. W., Griscom, H. P., Herrmann, V., Holl, K. D., Houghton, R. A., Larrosa, C., Lomax, G., Lucas, R., Madsen, P., Malhi, Y.,
- 387 Paquette, A., Parker, J. D., Paul, K., Routh, D., Roxburgh, S., Saatchi, S., van den Hoogen, J., Walker, W. S., Wheeler, C. E., Wood, S. A.,
- 388 Xu, L., and Griscom, B. W.: Mapping carbon accumulation potential from global natural forest regrowth, Nature, 585, 545-550, 2020.
- 389 Curtis, P. G., Slay, C. M., Harris, N. L., Tyukavina, A., and Hansen, M. C.: Classifying drivers of global forest loss, Science, 361, 1108-390 1111, 2018.
- 391 Davison, A. W. and Barnes, J. D.: Effects of ozone on wild plants, New Phytol, 139, 135-151, 1998.
- 392 Diaz, S., Kattge, J., Cornelissen, J. H., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I. C., Garnier, E., Bonisch,
- 393 G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., Chave, J., Wright, S. J., Sheremet'ev, S.
- 394 N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J. S., Gunther, A., Falczuk, V., Ruger, 395 N., Mahecha, M. D., and Gorne, L. D.: The global spectrum of plant form and function, Nature, 529, 167-171, 2016.
- 396 Farquhar, G. D., Caemmerer, S. V., and Berry, J. A.: A biochemical-model of photosynthetic CO₂ assimilation in leaves of C3 Species, 397 Planta, 149, 78-90, 1980.
- 398 Felzer, B. S., Cronin, T. W., Melillo, J. M., Kicklighter, D. W., and Schlosser, C. A.: Importance of carbon-nitrogen interactions and ozone 399 on ecosystem hydrology during the 21st century, J. Geophys. Res., 114, G01020, 2009.
- 400 Feng, Z., Agathokleous, E., Yue, X., Oksanen, E., Paoletti, E., Sase, H., Gandin, A., Koike, T., Calatayud, V., Yuan, X., Liu, X., De Marco, 401 A., Jolivet, Y., Kontunen-Soppela, S., Hoshika, Y., Saji, H., Li, P., Li, Z., Watanabe, M., and Kobayashi, K.: Emerging challenges of ozone 402 impacts on asian plants: actions are needed to protect ecosystem health, Ecosystem Health and Sustainability, 7, 1911602, 2021.
- 403 Feng, Z. Z., Buker, P., Pleijel, H., Emberson, L., Karlsson, P. E., and Uddling, J.: A unifying explanation for variation in ozone sensitivity 404
- among woody plants, Glob. Change Biol., 24, 78-84, 2018.
- 405 Feng, Z. Z., Sun, J. S., Wan, W. X., Hu, E. Z., and Calatayud, V.: Evidence of widespread ozone-induced visible injury on plants in Beijing,
- 406 China, Environ Pollut, 193, 296-301, 2014.
- 407 Fyllas, N. M., Quesada, C. A., and Lloyd, J.: Deriving Plant Functional Types for Amazonian forests for use in vegetation dynamics models, 408 Perspectives in Plant Ecology, Evolution and Systematics, 14, 97-110, 2012.
- 409 Gallagher, R. V., Falster, D. S., Maitner, B. S., Salguero-Gomez, R., Vandvik, V., Pearse, W. D., Schneider, F. D., Kattge, J., Poelen, J. H.,
- 410 Madin, J. S., Ankenbrand, M. J., Penone, C., Feng, X., Adams, V. M., Alroy, J., Andrew, S. C., Balk, M. A., Bland, L. M., Boyle, B. L.,





- 411 Bravo-Avila, C. H., Brennan, I., Carthey, A. J. R., Catullo, R., Cavazos, B. R., Conde, D. A., Chown, S. L., Fadrique, B., Gibb, H., Halbritter,
- 412 A. H., Hammock, J., Hogan, J. A., Holewa, H., Hope, M., Iversen, C. M., Jochum, M., Kearney, M., Keller, A., Mabee, P., Manning, P.,
- McCormack, L., Michaletz, S. T., Park, D. S., Perez, T. M., Pineda-Munoz, S., Ray, C. A., Rossetto, M., Sauquet, H., Sparrow, B., Spasojevic,
 M. J., Telford, R. J., Tobias, J. A., Violle, C., Walls, R., Weiss, K. C. B., Westoby, M., Wright, I. J., and Enquist, B. J.: Open Science
- 415 principles for accelerating trait-based science across the Tree of Life, Nat Ecol Evol, 4, 294-303, 2020.
- 416 Gelaro, R., McCarty, W., Suarez, M. J., Todling, R., Molod, A., Takacs, L., Randles, C. A., Darmenov, A., Bosilovich, M. G., Reichle, R.,
- 417 Wargan, K., Coy, L., Cullather, R., Draper, C., Akella, S., Buchard, V., Conaty, A., da Silva, A. M., Gu, W., Kim, G.-K., Koster, R., Lucchesi,
- 418 R., Merkova, D., Nielsen, J. E., Partyka, G., Pawson, S., Putman, W., Rienecker, M., Schubert, S. D., Sienkiewicz, M., and Zhao, B.: The
- 419 Modern-Era Retrospective Analysis for Research and Applications, Version 2 (MERRA-2), J Climate, 30, 5419-5454, 2017.
- Henry, C., John, G. P., Pan, R., Bartlett, M. K., Fletcher, L. R., Scoffoni, C., and Sack, L.: A stomatal safety-efficiency trade-off constrains
 responses to leaf dehydration, Nat Commun, 10, 3398, 2019.
- Herdt, R. W.: The state of food and agriculture, 2003-2004: Agricultural biotechnology: Meeting the needs of the poor?, Agricultural
 Economics, 32, 109-+, 2005.
- 424 Kattge, J. and Diaz, S. and Lavorel, S. and Prentice, C. and Leadley, P. and Bonisch, G. and Garnier, E. and Westoby, M. and Reich, P. B.
- 425 and Wright, I. J. and Cornelissen, J. H. C. and Violle, C. and Harrison, S. P. and van Bodegom, P. M. and Reichstein, M. and Enquist, B. J.
- 426 and Soudzilovskaia, N. A. and Ackerly, D. D. and Anand, M. and Atkin, O. and Bahn, M. and Baker, T. R. and Baldocchi, D. and Bekker, 427 R. and Blanco, C. C. and Blonder, B. and Bond, W. J. and Bradstock, R. and Bunker, D. E. and Casanoves, F. and Cavender-Bares, J. and
- 428 Chambers, J. Q. and Chapin, F. S. and Chave, J. and Coomes, D. and Cornwell, W. K. and Craine, J. M. and Dobrin, B. H. and Duarte, L.
- 429 and Durka, W. and Elser, J. and Esser, G. and Estiarte, M. and Fagan, W. F. and Fang, J. and Fernandez-Mendez, F. and Fidelis, A. and
- 430 Finegan, B. and Flores, O. and Ford, H. and Frank, D. and Freschet, G. T. and Fyllas, N. M. and Gallagher, R. V. and Green, W. A. and
- 431 Gutierrez, A. G. and Hickler, T. and Higgins, S. I. and Hodgson, J. G. and Jalili, A. and Jansen, S. and Joly, C. A. and Kerkhoff, A. J. and
- 432 Kirkup, D. and Kitajima, K. and Kleyer, M. and Klotz, S. and Knops, J. M. H. and Kramer, K. and Kuhn, I. and Kurokawa, H. and Laughlin,
- 433 D. and Lee, T. D. and Leishman, M. and Lens, F. and Lenz, T. and Lewis, S. L. and Lloyd, J. and Llusia, J. and Louault, F. and Ma, S. and 434 Mahecha, M. D. and Manning, P. and Massad, T. and Medlyn, B. E. and Messier, J. and Moles, A. T. and Muller, S. C. and Nadrowski, K.
- 435 and Naeem, S. and Niinemets, U. and Nollert, S. and Nuske, A. and Ogaya, R. and Oleksyn, J. and Onipchenko, V. G. and Onoda, Y. and
- 436 Ordonez, J. and Overbeck, G. and Ozinga, W. A. and Patino, S. and Paula, S. and Pausas, J. G. and Penuelas, J. and Phillips, O. L. and Pillar,
- 437 V. and Poorter, H. and Poorter, L. and Poschlod, P. and Prinzing, A. and Proulx, R. and Rammig, A. and Reinsch, S. and Reu, B. and Sack,
- 438 L. and Salgado-Negre, B. and Sardans, J. and Shiodera, S. and Shipley, B. and Siefert, A. and Sosinski, E. and Soussana, J. F. and Swaine,
- 439 E. and Swenson, N. and Thompson, K. and Thornton, P. and Waldram, M. and Weiher, E. and White, M. and White, S. and Wright, S. J. 440 and Yguel, B. and Zaehle, S. and Zanne, A. E. and Wirth, C.: TRY - a global database of plant traits, Global Change Biol, 17, 2905-2935,
- 2011.
 Li, D., Wang, X., Zheng, H., Zhou, K., Yao, X., Tian, Y., Zhu, Y., Cao, W., and Cheng, T.: Estimation of area- and mass-based leaf nitrogen
- contents of wheat and rice crops from water-removed spectra using continuous wavelet analysis, Plant Methods, 14, 2018.
 Li, P., Calatayud, V., Gao, F., Uddling, J., and Feng, Z. Z.: Differences in ozone sensitivity among woody species are related to leaf
- 445 morphology and antioxidant levels, Tree Physiol., 36, 1105-1116, 2016.
- Li, P., Feng, Z., Catalayud, V., Yuan, X., Xu, Y., and Paoletti, E.: A meta-analysis on growth, physiological, and biochemical responses of woody species to ground-level ozone highlights the role of plant functional types, Plant Cell Environ, 40, 2369-2380, 2017.
- Li, S., Moller, C. A., Mitchell, N. G., Lee, D., Sacks, E. J., and Ainsworth, E. A.: Testing unified theories for ozone response in C-4 species,
 Global Change Biol, 28, 3379-3393, 2022.
- 450 Lombardozzi, D., Levis, S., Bonan, G., Hess, P. G., and Sparks, J. P.: The Influence of Chronic Ozone Exposure on Global Carbon and 451 Water Cycles, J Climate, 28, 292-305, 2015.
- Massman, W. J., Musselman, R. C., and Lefohn, A. S.: A conceptual ozone dose-response model to develop a standard to protect vegetation,
 Atmos Environ, 34, 745-759, 2000.
- 454 Mills, G., Sharps, K., Simpson, D., Pleijel, H., Broberg, M., Uddling, J., Jaramillo, F., Davies, W. J., Dentener, F., Van den Berg, M.,
- 455 Agrawal, M., Agrawal, S. B., Ainsworth, E. A., Buker, P., Emberson, L., Feng, Z. Z., Harmens, H., Hayes, F., Kobayashi, K., Paoletti, E.,
- 456 and Van Dingenen, R.: Ozone pollution will compromise efforts to increase global wheat production, Global Change Biol, 24, 3560-3574,
 457 2018a.
- 458 Mills, G., Sharps, K., Simpson, D., Pleijel, H., Frei, M., Burkey, K., Emberson, L., Uddling, J., Broberg, M., Feng, Z., Kobayashi, K., and
- Agrawal, M.: Closing the global ozone yield gap: Quantification and cobenefits for multistress tolerance, Glob Chang Biol, 24, 4869-4893,
 2018b.
- 461 Moreno-Martinez, A., Camps-Valls, G., Kattge, J., Robinson, N., Reichstein, M., van Bodegom, P., Kramer, K., Cornelissen, J. H. C., Reich,
- 462 P., Bahn, M., Niinemets, U., Penuelas, J., Craine, J. M., Cerabolini, B. E. L., Minden, V., Laughlin, D. C., Sack, L., Allred, B., Baraloto, C.,
- Byun, C., Soudzilovskaia, N. A., and Running, S. W.: A methodology to derive global maps of leaf traits using remote sensing and climate
 data, Remote Sens Environ, 218, 69-88, 2018.
- 465 Mukherjee, A., Yadav, D. S., Agrawal, S. B., and Agrawal, M.: Ozone a persistent challenge to food security in India: Current status and 466 policy implications, Current Opinion in Environmental Science & Health, 19, 100220, 2021.





- Poorter, H., Niinemets, U., Poorter, L., Wright, I. J., and Villar, R.: Causes and consequences of variation in leaf mass per area (LMA): a
 meta-analysis, New Phytol, 182, 565-588, 2009.
- 469 Reich, P. B.: The world-wide 'fast-slow' plant economics spectrum: a traits manifesto, J Ecol, 102, 275-301, 2014.
- 470 Reich, P. B. and Amundson, R. G.: AMBIENT LEVELS OF OZONE REDUCE NET PHOTOSYNTHESIS IN TREE AND CROP 471 SPECIES, Science, 230, 566-570, 1985.
- 472 Reich, P. B., Ellsworth, D. S., and Walters, M. B.: Leaf structure (specific leaf area) modulates photosynthesis-nitrogen relations: evidence
 473 from within and across species and functional groups, Funct Ecol, 12, 948-958, 1998.
- 474 Reich, P. B., Ellsworth, D. S., Walters, M. B., Vose, J. M., Gresham, C., Volin, J. C., and Bowman, W. D.: Generality of leaf trait 475 relationships: A test across six biomes, Ecology, 80, 1955-1969, 1999.
- Reich, P. B., Walters, M. B., and Ellsworth, D. S.: From tropics to tundra: Global convergence in plant functioning, P Natl Acad Sci USA,
 94, 13730-13734, 1997.
- 478 Richards, B. L., Middleton, J. T., and Hewitt, W. B.: Air Pollution With Relation to Agronomic Crops: V. Oxidant Stipple of Grape, Agron
 479 J, 50, 559-561, 1958.
- 480 Richards, R. A.: Selectable traits to increase crop photosynthesis and yield of grain crops, J Exp Bot, 51, 447-458, 2000.
- 481 Shipley, B., Lechowicz, M. J., Wright, I., and Reich, P. B.: Fundamental trade-offs generating the worldwide leaf economics spectrum, 482 Ecology, 87, 535-541, 2006.
- 483 Sitch, S., Cox, P. M., Collins, W. J., and Huntingford, C.: Indirect radiative forcing of climate change through ozone effects on the land-484 carbon sink, Nature, 448, 791-794, 2007.
- Tiwari, S., Grote, R., Churkina, G., and Butler, T.: Ozone damage, detoxification and the role of isoprenoids new impetus for integrated models, Funct Plant Biol, 43, 324-336, 2016.
- 487 Turnock, S. T., Wild, O., Dentener, F. J., Davila, Y., Emmons, L. K., Flemming, J., Folberth, G. A., Henze, D. K., Jonson, J. E., Keating, T.
- 488 J., Kengo, S., Lin, M., Lund, M., Tilmes, S., and O'Connor, F. M.: The impact of future emission policies on tropospheric ozone using a 489 parameterised approach, Atmos Chem Phys, 18, 8953-8978, 2018.
- 490 Wang, K. and Shangguan, Z.: Photosynthetic characteristics and resource utilization efficiency of maize (Zea maysL.) and millet (Setaria 491 italicaL.) in a semi-arid hilly loess region in China, New Zeal J Crop Hort, 38, 247-254, 2010.
- 492 Wittig, V. E., Ainsworth, E. A., Naidu, S. L., Karnosky, D. F., and Long, S. P.: Quantifying the impact of current and future tropospheric
- 493 ozone on tree biomass, growth, physiology and biochemistry: a quantitative meta-analysis, Global Change Biol, 15, 396-424, 2009.
- Wright, I. J., Westoby, M., and Reich, P. B.: Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different
 consequences for leaf life span, J Ecol, 90, 534-543, 2002.
- 496 Wu, Y., Gong, W., Wang, Y., Yong, T., Yang, F., Liu, W., Wu, X., Du, J., Shu, K., Liu, J., Liu, C., and Yang, W.: Leaf area and 497 photosynthesis of newly emerged trifoliolate leaves are regulated by mature leaves in soybean, J Plant Res, 131, 671-680, 2018.
- Yue, X. and Unger, N.: The Yale Interactive terrestrial Biosphere model version 1.0: description, evaluation and implementation into NASA
 GISS ModelE2, Geosci Model Dev, 8, 2399-2417, 2015.
- Zalles, V., Hansen, M. C., Potapov, P. V., Parker, D., Stehman, S. V., Pickens, A. H., Parente, L. L., Ferreira, L. G., Song, X.-P., Hernandez Serna, A., and Kommareddy, I.: Rapid expansion of human impact on natural land in South America since 1985, Sci Adv, 7, eabg1620,
 2021.
- 502
- 504
- . .

- 506
- 507
- 508
- 509
- 507
- 510
- 511





512

513 **Table 1.** Summary of simulations.

514

Experiment ^a	Method	Thresholds ^a $(x \text{ or } y)$	LMA format	LMA map	Optimal (<i>a</i> or <i>a</i> _{PFT})	Tests (<i>a</i> or <i>a</i> _{PFT})
YIBs-LMA	Mass- based	<i>x</i> =0.019	gridded	M2018	<i>a</i> =3.5 (Table S3)	five tests (<i>a</i> =2.5, 3, 3.5, 4, 4.5)
YIBs-LMA_PFT		<i>x</i> =0.019	PFT- specific	M2018	<i>a</i> =2.0 (Table S4)	five tests (<i>a</i> =2, 2.5, 3, 3.5, 4)
YIBs-LMA_T		<i>x</i> =0.006	gridded	M2018	<i>a</i> =3.0 (Table S5)	five tests (<i>a</i> =2, 2.5, 3, 3.5, 4)
YIBs-LMA_B2017		<i>x</i> =0.019	gridded	B2017	<i>a</i> =2.8 (Table S6)	five tests (<i>a</i> =2, 2.5, 2.8, 3, 3.5)
YIBs-S2007_adj	Area- based	8 values for <i>y</i> (Table S7)	/	/	8 values for <i>a_{PFT}</i> (Table S7)	40 tests (five each for 8 PFTs)

515

516 ^a Units of thresholds are nmol $g^{-1} s^{-1}$ for x and nmol $m^{-2} s^{-1}$ for y

517 ^b Units of key parameters are nmol⁻¹ s g for *a* and nmol⁻¹ m² s for a_{PFT}





519

520



521

Figure 1. Area-based (top) or mass-based (bottom) DRRs for the YIBs-LMA experiment. Three tests 522 from the YIBs-LMA experiment all adopt x=0.019 nmol g⁻¹ s⁻¹ and gridded LMA from M2018 with 523 parameter $a=2.5, 3.5, 4.5 \text{ nmol}^{-1} \text{ s g}$, respectively. Each dot represents estimated POD-R_{GPP} (POD_{y=1} for 524 (a)-(c), $POD_{x=0.019}$ for (d)-(e)) at a grid with corresponding PFT. The PFT-specific regressions between 525 area- or mass- based POD and R_{GPP} are displayed with solid lines shown in legend. Regression 526 relationships of all PFTs are displayed in black dash line with coefficients of determination (R²) denoted 527 528 on each panel. Note the differences of ranges in x axis among PFTs. The YIBs-LMA experiment is summarized in Table 1. 529







531

Figure 2. Comparison between S_O (% per mmol m⁻²) and S_S (% per mmol m⁻²) for the YIBs-LMA experiment. Five tests from the YIBs-LMA experiment all adopt *x*=0.019 nmol g⁻¹ s⁻¹ and gridded LMA from M2018 but with varied parameter *a* from (a) 2.5 to (e) 4.5 nmol⁻¹ s g. S_O are from Table S1. S_S are derived as the slope between R_{GPP} and POD_y. The linear regression (dashed lines), normalized mean biases (NMB), and correlation coefficient (r) between S_S and S_O for varied PFTs are shown on each panel. The S_S and S_O of CRO are derived using POD_{y=6} while other PFTs use POD_{y=1}. The YIBs-LMA experiment is described in Table 1.







Figure 3. Comparisons of observed and simulated dose-response relationships. Simulated PFT-specific 541 DRRs are derived from YIBs-LMA with gridded LMA from M2018, x=0.019 nmol g⁻¹ s⁻¹, and a=3.5542 nmol⁻¹ s g. Each dot represents results from a gridcell with corresponding PFT. The regressions between 543 relative GPP percentage (R_{GPP}) and leaf area-based stomatal O₃ uptake fluxes (POD_{y=1} for natural PFTs 544 and POD_{v=6} for crops) are shown for observations (red, see Table S1) and simulations (blue) with slopes 545 of DRRs denoted as So and Ss, respectively. So are missing for (d) cold and (e) arid shrubs. Coefficients 546 of determination (R²) of simulations are displayed in each panel. Note the differences of ranges in x axis 547 among PFTs (PFTs are shown in Fig. S2). 548







Figure 4. Global O₃ vegetation damage simulated with the LMA-based scheme. Results shown are the (a) GPP reduction percentages by O₃ simulated with the YIBs-LMA framework (gridded LMA from M2018, x=0.019 nmol g⁻¹ s⁻¹, and a=3.5 nmol⁻¹ s g), and (b) their differences compared to the predictions from YIBs-S2007_adj simulation. Blue (red) patches indicate the regions where damages predicted in YIBs-LMA are lower (higher) than those in YIBs-S2007_adj.







Figure 5. Global O₃-induced GPP reductions simulated in four supporting experiments. All damage maps are based on optimal parameters shown in Table 1. The spatial correlation coefficients between YIBs-LMA and these supporting simulations are shown on each panel as well as the global average damage percentage of each map. Simulations are described in Table 1.







Figure 6. Comparison of S_S/S_O among supporting experiments. Individual ratios for (b) different PFTs are grouped to the boxplot in (a). All experiments adopt optimal parameters shown in Table 1.



Geoscientific Model Development





Figure 7. Relationships between O_3 sensitivity and LMA. (a) Simulated O_3 sensitivity (S_5) at each grid is compared with LMA for different PFTs. Gridded S_5 is derived as GPP change per unit POD_{y=1} from the YIBs-LMA simulation. Each point represents the value in a grid cell with a dominant PFT. (b) The PFT-level relationships between LMA and O_3 sensitivity are grouped as boxplots, which indicate the median, 25th percentile, and 75th percentile of y-axis variables within the same PFT. The width of boxplots represents one standard deviation of LMA for a specific PFT.







577 Figure 8. Illustration of the relationships between leaf trade-off strategy and its sensitivity to O₃

578