Emergence of the physiological effects of elevated CO2 on land-atmosphere exchange of carbon and water

Chunhui Zhan¹, René Orth¹, Mirco Migliavacca¹, Sönke Zaehle², Markus Reichstein¹, Jan Engel², Anja Rammig³, and Alexander J Winkler¹

¹Department for Biogeochemical Integration, Max Planck Institute for Biogeochemistry, Jena, Germany

²Department of Biogeochemical Signals, Max Planck Institute for Biogeochemistry, Jena, Germany

³Land Surface-Atmosphere Interactions, Technical University of Munich, TUM School of Life Sciences Weihenstephan, 85354 Freising, GermanyLand Surface-Atmosphere Interactions

November 21, 2022

Abstract

Elevated atmospheric CO2 (eCO2) influences the carbon assimilation rate and stomatal conductance of plants, and thereby can affect the global cycles of carbon and water. However, the extent to which these physiological effects of eCO2 influence the land-atmosphere exchange of carbon and water is uncertain. In this study, we aim at developing a method to detect the emergence of the physiological CO2 effects on various variables related to carbon and water fluxes. We use a comprehensive process-based land surface model QUINCY (QUantifying Interactions between terrestrial Nutrient CYcles and the climate system) to simulate the leaf-level effects of increasing atmospheric CO2 concentrations and their century-long propagation through the terrestrial carbon and water cycles across different climate regimes and biomes. We then develop a statistical method based on the signal-to-noise ratio to detect the emergence of the eCO2 effects. The signal in gross primary production (GPP) emerges at relatively low eCO2 (Δ[°O2] ~ 20 ππμ) ωηερε τηε λεαφ αρεα ινδεξ (ΛΑΙ) ις ρελατιελψ ηιγη. δμπαρεδ το ΓΠΠ, τηε εΌ2 εφφεςτ ςαυσινγ ρεδυςεδ 28 τρανσπιρατιον ωατερ φλυξ (νορμαλιζεδ το λεαφ αρεα) εμεργες ονλψ ατ ρελατιελψ ηιγη Ό2 ινςρεασε (Δ [$^{\circ}$ O2] >> 40 ππμ), δυε το τηε ηιγη σενσιτιιτψ το ςλιματε αριαβιλιτψ ανδ τηυς λοωερ σιγναλ-το-νοισε ρατιο. Ιν γενεραλ, της ρεσπονσε το εΌ2 ις δετεςταβλε εαρλιερ φορ αριαβλες οφ της ςαρβον ςψελε τηαν της ωατερ εψελε, ωηεν πλαντ προδυετιιτψ ις νοτ λιμιτεδ βψ ςλιματις ςονστραιντς, ανδ στρονγερ ιν φορεστ-δομινατεδ ρατηερ τηαν ιν γρασσ- δομινατεδ εςοσψστεμς. Ουρ ρεσυλτς προιδε α στεπ τοωαρδς ωηεν ανδ ωηερε ωε εξπεςτ το δετεςτ πηψσιολογιςαλ Ό2 εφφεςτς ιν ιν-σιτυ φλυξ μεασυρεμεντς, ηοω το δετεςτ τηεμ ανδ ενςουραγε φυτυρε εφφορτς το ιμπροε τηε υνδερστανδινγ ανδ χυαντιφιζατιον οφ τηεσε εφφεςτς ιν οβσερατιονς οφ τερρεστριαλ ςαρβον ανδ ωατερ δψναμιςς.

Emergence of the physiological effects 1 of elevated CO₂ on land-atmosphere

exchange of carbon and water 3

- Chunhui Zhan¹, René Orth¹, Mirco Migliavacca^{1,4}, Sönke Zaehle², Markus Reichstein¹, Jan 4
- Engel², Anja Rammig³ and Alexander J. Winkler¹ 5
- 6

2

- 7 ¹Department for Biogeochemical Integration, Max Planck Institute for Biogeochemistry, Jena, Germany 8
- 9 ² Department of Biogeochemical Signals, Max Planck Institute for Biogeochemistry, Jena, Germany 10
- ³Land Surface-Atmosphere Interactions, Technical University of Munich, TUM School of Life 11
- 12 Sciences Weihenstephan, 85354 Freising, Germany
- 13 ⁴ European commission, Joint Research Centre, Ispra (VA), Italy

Abstract 14

Elevated atmospheric CO₂ (eCO₂) influences the carbon assimilation rate and 15 16 stomatal conductance of plants, and thereby can affect the global cycles of carbon and 17 water. However, the extent to which these physiological effects of eCO₂ influence the land-atmosphere exchange of carbon and water is uncertain. In this study, we aim at 18 19 developing a method to detect the emergence of the physiological CO₂ effects on 20 various variables related to carbon and water fluxes. We use a comprehensive process-based land surface model QUINCY (QUantifying Interactions between 21 terrestrial Nutrient CYcles and the climate system) to simulate the leaf-level effects of 22 increasing atmospheric CO₂ concentrations and their century-long propagation 23 through the terrestrial carbon and water cycles across different climate regimes and 24 biomes. We then develop a statistical method based on the signal-to-noise ratio to 25 26 detect the emergence of the eCO₂ effects. The signal in gross primary production (GPP) emerges at relatively low eCO_2 ($\Delta[CO_2] \sim 20$ ppm) where the leaf area index 27

(LAI) is relatively high. Compared to GPP, the eCO₂ effect causing reduced 28 transpiration water flux (normalized to leaf area) emerges only at relatively high CO₂ 29 increase (Δ [CO₂] >> 40 ppm), due to the high sensitivity to climate variability and thus 30 31 lower signal-to-noise ratio. In general, the response to eCO₂ is detectable earlier for 32 variables of the carbon cycle than the water cycle, when plant productivity is not limited by climatic constraints, and stronger in forest-dominated rather than in grass-33 34 dominated ecosystems. Our results provide a step towards when and where we expect 35 to detect physiological CO₂ effects in in-situ flux measurements, how to detect them 36 and encourage future efforts to improve the understanding and guantification of these effects in observations of terrestrial carbon and water dynamics. 37

38 1 Introduction

39 Plants are tightly coupled to the ambient atmosphere through their exchange of 40 energy, water and carbon (Gentine et al., 2019). Through this coupling, plants play an essential role in controlling the global cycles of carbon and water, and also modulate 41 42 Earth's surface energy balance (Gedney et al., 2006; Williams and Torn, 2015; Friedlingstein et al., 2019). Changing atmospheric conditions such as rising air 43 temperature, or increasing dryness in turn directly impact on plants and their 44 functioning (Reichstein et al., 2013; Novick et al., 2016; Bastos et al., 2020). Also 45 46 changes in the atmospheric composition, such as elevated atmospheric CO₂ (eCO₂) 47 can alter plant productivity, for example by stimulating carbon assimilation and by 48 reducing stomatal conductance (Ainsworth and Long, 2005; Norby and Zak, 2011; 49 Walker et al., 2021). As a result, the light-use efficiency (LUE; Drake et al., 1997) and 50 the water-use efficiency of plants (WUE; Peñuelas et al., 2011; Ueyama et al., 2020) increase under eCO₂. The combined effect is referred to as the CO₂ fertilization effect
(Körner et al., 2007; Walker et al., 2021).

Plant leaves respond directly to eCO₂ through the physiological mechanisms 53 54 associated to the CO₂ fertilization effect, which could potentially translate into changes of gross primary productivity (GPP) and transpiration (Tr) that can propagate further 55 into the carbon and water cycles (Fernández-Martínez et al., 2017; Lemordant et al., 56 2018; Walker et al., 2021). Specifically, the eCO₂ effect alters the carbon cycle by 57 triggering changes in GPP resulting in changes in net primary production (NPP) and 58 59 various aspects of biomass production, accumulation and allocation (e.g., leaves or roots). The increased biomass production can potentially contribute to an increased 60 leaf area index (LAI). Observational evidence suggests that this effect can vary 61 62 substantially across different biomes and plant functional types (Norby and Zak, 2011; 63 De Kauwe et al., 2014; Winkler et al., 2021). The water cycle is affected as eCO₂ is 64 triggering changes in the leaf-level Tr flux which controls the largest fraction of the land-atmosphere water exchange (Good et al., 2015). The eCO₂-induced change of 65 Tr implies a potential influence on other components in the water cycle, such as soil 66 67 evaporation, run-off, and consequently soil moisture (Leuzinger and Körner, 2007; 68 Lemordant et al., 2018). However, reduced transpiration at the leaf level due to reduced stomatal conductance and stomatal density in response to eCO₂ (Woodward 69 70 and Kelly, 1995; Ainsworth and Rogers, 2007) could be offset by a simultaneous 71 increase in leaf area, and thus transpiration at canopy level as more carbon is invested 72 in leaf growth in response to eCO₂ (Wullschleger et al., 2002). These competing 73 effects of eCO₂ could potentially compensate each other, resulting in a non-detectable 74 effect on the water cycle. Similar but in an opposite way, the increasing leaf area 75 enhances GPP by controlling light interception (McCarthy et al., 2006).

76 The quantification of the effects of eCO₂ on carbon and water cycles in experiments 77 and observations remain inconsistent. The intrinsic WUE inferred from 21 flux site measurements shows strong increase (Keenan et al., 2013), while the study by 78 79 Knauer et al. (2017) indicates a smaller magnitude of WUE response at a recent large scale. Increased biomass is found in many Free-Air CO₂ Enrichment (FACE) 80 experiments (Walker et al., 2019). However, tree-ring studies indicate the increased 81 intrinsic WUE does not translate into the increased tree biomass (Peñuelas et al., 82 2011; van der Sleen et al., 2015). The diverse response of plant physiology to eCO₂ 83 84 is observed in many other aspects. Results from field experiments show the magnitude of eCO₂ stimulation on carbon assimilation rate varies considerably across species 85 and experimental conditions (Norby et al., 1999; Leakey et al., 2009; Norby and Zak, 86 87 2011; Walker et al., 2021). Meta-analysis indicates that stomatal conductance in 88 young trees show stronger response to eCO₂ than old trees, and deciduous forest show stronger response than conifer forest (Medlyn et al., 2001). Furthermore, 89 90 photosynthesis in C4 plants is close to being saturated, while plants in the C3 carbon pathway are expected to show a greater increase in carbon assimilation rate (Kramer, 91 1981; Ainsworth and Rogers, 2007; Leakey et al., 2009). Though C4 plants may have 92 more potential response to eCO₂ associated with high WUE (Way et al., 2014). 93 94 Overall, the uncertain strength of eCO₂ effects across different climate zones and 95 biomes prevents us from better understanding the governing processes, but this is necessary to anticipate future changes of carbon and water fluxes in the system. 96

97 This study aims to develop a methodology that would be helpful to define the 98 detectable imprint of CO₂ on land-atmosphere fluxes of carbon and water. Such a 99 detection is challenging with real-world data, mostly due to confounding factors 100 impacting on long-term plant productivity, such as climatic variability, nitrogen

101 deposition, and land cover change (McCarthy et al., 2010; Schimel et al., 2015; 102 Fernández-Martínez et al., 2017; Liu et al., 2021). FACE experiments provide the 103 opportunities to observe the response of ecosystems to eCO_2 in the field exposed in 104 open-air conditions (Ainsworth and Long, 2005). Nevertheless, in these experiments, 105 ecosystems are pushed into an "accelerating mode" where plants are exposed to a 106 much higher rate of CO_2 concentration increase (\approx 550 ppm) in a short time period

107 while the climate conditions are changing at a relatively slow speed. Process-based models provide the opportunity to conduct factorial experiments to isolate the role of 108 109 individual drivers, which allows us to test a statistical trend-detection method. Here, 110 we perform three simulations with the terrestrial biosphere model QUINCY 111 (QUantifying Interactions between terrestrial Nutrient CYcles and the climate system; Thum et al., 2019) to isolate the eCO₂ effects: (i) a reference simulation with transient 112 113 CO₂ concentrations and observation-based meteorological forcing, (ii) a simulation where the CO₂ is kept constant at the level of 1901 while the meteorological forcing is 114 115 identical to the reference simulation; and (iii) a simulation with the same set up of (i) 116 but CO₂ is kept constant after the year 1988 at the level of 1988. The simulation (iii) is 117 used to test our method in the recent time period, when the FLUXNET observations 118 start to be recorded. Analyzing the differences of carbon and water fluxes between 119 both simulations, we develop a statistical method to detect the time of emergence of significant eCO₂ effects on these fluxes given their natural variability. In other words, 120 121 we seek to identify the point in time the eCO₂ effects are distinguishable from short-122 term and long-term climate effects. We concentrate on the two variables which are 123 most directly affected by rising CO₂, GPP and Tr at annual, seasonal and diurnal 124 scales. To exclude the potential compensation effect of increasing LAI, we normalize Tr by LAI (Tr_{norm}) to obtain the transpiration flux per leaf area. Subsequently, we 125

analyze eCO₂ effects on ecosystem properties (Table 1) which are important in the
carbon and water cycle and investigate controls of the emergence of the eCO₂ effects.
We also include Earth system models from the most recent Coupled Model
Intercomparison Project (CMIP6) to examine whether the controls of the emergence
of the eCO₂ effects are exclusive in the QUINCY model.

131 2 Materials and Methods

132 2.1 QUINCY model

133 2.1.1 Model description

134 The terrestrial ecosystem model, QUINCY (QUantifying Interactions between terrestrial Nutrient CYcles and the climate system; Thum et al., 2019), is designed to 135 represent the coupled carbon, nitrogen, and phosphorus cycles and their interactions 136 137 with energy and water balances in terrestrial ecosystems. QUINCY simulates half-138 hourly carbon, water and energy fluxes as well as longer-term ecosystem dynamics across climate regimes and different plant functional types (PFTs), representing 139 140 different plant growth forms (tree, grass), leaf types (leaves, needles) and phenology (evergreen, cold and drought deciduous, perennial). Calculation of coupled 141 photosynthesis (Kull and Kruijt, 1998) and stomatal conductance (Medlyn et al., 2011) 142 are taking for sunlit and shaded leaves separately along the vertical canopy gradient 143 144 of light, foliar chlorophyll and photosynthetic N. QUINCY accounts for limitations of 145 photosynthesis by light, CO₂, temperature and water availability. GPP at the canopy 146 level is integrated from leaf-level gross photosynthesis. The simulated diurnal and seasonal patterns of GPP have been evaluated against a number of benchmarks, 147

148 including several FLUXNET sites. Leaf area development is dynamically dependent 149 on plant production (and thereby its response to changing atmospheric CO₂, climate and water availability) as well as stand structural development and turnover through 150 151 mortality and establishment. Transpiration is calculated as a function of the stomatal conductance of the canopy, aerodynamic conductance, and other parameters in terms 152 153 of air density and humidity. Soil physics, moisture and biogeochemistry are modelled 154 for 15 layers with exponentially increasing depth. QUINCY calculates the litter and soil 155 organic matter turnover by first-order kinetics with temperature and moisture 156 dependencies. For more detailed explanations of the process representations in QUINCY, please refer to the model description by Thum et al. (2019). 157

158 2.1.2 Model setup

159 2.1.2.1 Boundary conditions and meteorological forcing

160 The QUINCY model is a 1-D model applied at individual sites (339 sites) distributed 161 across climate zones and biomes for the time period 1901-2018. As an offline land surface model, QUINCY takes time-dependent observation-based meteorological 162 163 forcing variables as input such as short- and longwave radiation, air temperature, 164 precipitation, vapor pressure deficit (VPD), atmospheric CO₂ concentration, as well as other boundary conditions such as geographical coordinates, PFTs, and soil physical 165 and chemical parameters. At each site, a specific boundary condition and 166 167 meteorological forcing is taken from the Climate Research Unit and Japanese reanalysis product (CRU JRA V2.1; Harris, 2020), and disaggregated to the model 168 time step (half-hourly) using the statistical weather generator (Zaehle and Friend, 169 170 2010). The annual atmospheric CO₂ concentration is obtained from the Global Carbon 171 Project (Le Quéré et al., 2018). Soil physical and chemical properties are derived from soil texture (Saxton and Rawls, 2006). The texture data are taken from the nearest grid cell of SoilGrids dataset (Hengl et al., 2017). To improve the interpretability of the model simulations with respect to the occurrence of the eCO₂ signal, we reduce the model complexity and set the soil-soluble NH₄, NO₃ and PO₄ concentrations at a prescribed level so that the plant growth is not limited by the nutrient availability, and disregard the N and P deposition in the model.

178 2.1.2.2 Model simulation experiments for hypothesis testing

179 We conduct three factorial model experiments to disentangle the effects of eCO₂ from 180 other drivers: (a) Transient-CO₂ experiment. This simulation can be considered as a 181 historical run that aims to approximate the observed system and thus takes the 182 transient climate and CO₂ concentration for the period 1901-2018 as forcing. The 183 transient-CO₂ experiment simulates an increase in atmospheric CO₂ of 110.63 ppm over 118 years; (b) Constant-CO₂ experiment. This simulation includes the same 184 transient climate as the transient-CO₂ experiment. However, the atmospheric CO₂ 185 186 concentration does not change and is fixed to the initial value of 1901 (296.8 ppm) for the entire simulation period. The climate forcing data contains the effects of rising CO₂. 187 188 (c) Freeze-CO₂ experiment. Here, the atmospheric CO₂ increases until 1988, as in the 189 transient-CO₂ experiment, but is then kept constant at this value in the years thereafter. The year 1988 was chosen as the time close to the setup of the first 190 FLUXNET sites (Baldocchi et al., 2001). 191

192 2.2 Statistical analysis

193 2.2.1 The effect of elevated CO₂ on annual average GPP and Tr_{norm}

We first calculate the difference in annual average values of GPP and normalized 194 195 transpiration ($Tr_{norm} = Tr / LAI$) between the transient-CO₂ and the constant-CO₂ 196 experiments. The difference indicates the eCO₂ effect on the target variable for the period 1901-2018. We cluster the sites based on site-PFT in four vegetation groups: 197 198 Tropical Forest, Temperate Forest, Boreal Forest and Grasses (Table S1). We further classify the sites of each vegetation group into three temperature classes, "hot", 199 "warm", and "cold" based on the quantiles of long-term mean 2m air temperature 200 201 between the sites in each group. Subdividing the temperature classes further based 202 on the long-term mean annual precipitation ("low", "middle", and "high"), we are able 203 to assess the role of water availability in controlling the variability in GPP and 204 normalized transpiration. While the CO₂-induced change of LAI compensates the 205 reduced leaf-level water loss at canopy Tr, it governs GPP in an opposite way. The 206 structural change of increased LAI increases the amount of absorbed photosynthetically active radiation (APAR) and therefore vegetation productivity. We 207 208 also evaluate the eCO₂ effect on annual average LUE (LUE = GPP / APAR). The part 209 of increased GPP related to increased LAI can be thus disentangled.

210 2.2.2 Emergence of the elevated CO₂ effects

Based on the CO₂ fertilization effect, we hypothesize that the continuous CO₂ increase over a long period of time exerts a significant influence on the ecosystem (e.g., GPP), which stands out as the eCO₂ effect from natural variability and other factors after a given time and strength of atmospheric CO₂ concentration increase. We define the 215 emergence of the eCO₂ effects (EoC, ppm) as the change in CO₂ concentration 216 $(\Delta[CO_2])$ required so that the time series of a simulated variable in the transient-CO₂ 217 experiment diverges significantly from the constant-CO₂ experiment. The significant 218 divergence between the two time series is defined by the point in time when the signal 219 exceeds the noise. The noise is intended as the interannual variability of the signal 220 around the long-term changes. We retrieve the signal and noise from the linear fit in 221 the historical time period for each experiment. The calculation of EoC consists of 4 222 steps: (1) For each site, we calculate annual averages for the target variable (e.g., GPP) from daily model output for both transient-CO₂ and constant-CO₂ experiments 223 224 for the time period 1901-2018; (2) We apply linear least squares regressions to retrieve 225 the trend in the time series of the target variable from both transient- and constant-226 CO₂ experiments, respectively, over a given time period (Fig.1). We start with the time 227 period 1901-1910 and iteratively expand this time period year by year by advancing 228 the final year of the time window. For each time period, we compute the linear trend 229 and its uncertainty. Accordingly, we obtain an estimate of the trend and its uncertainties for a total of n = 108 points in time for each experiment at each site. The 230 231 trend b and its standard error σ_b in the linear regression model are given by (Weisstein, n.d.): 232

233
$$b = \frac{\sum_{i=1}^{n} (x_i - \overline{x})(y_i - \overline{y})}{\sum_{i=1}^{n} (x_i - \overline{x})^2}$$

234
$$\sigma_b = \sqrt{\frac{(\sum_{i=1}^n (y_i - \overline{y})^2 - (\sum_{i=1}^n (x_i - \overline{x})(y_i - \overline{y}) \times b)/(n-2)}{\sum_{i=1}^n (x_i - \overline{x})^2}}$$

235 Where *x* is the year at time step *i*, and *y* is the value of target variable at the year x_i ; 236 (3) The signal is retrieved as the absolute difference in the regression slopes Δb (*b* in 237 transient-CO₂ minus *b* in constant-CO₂) as a function of time, while the noise is 238 estimated based on twice the sum of two σ_b from the transient-CO₂ and constant-CO₂ 239 experiments; (4) The time of emergence is determined by the year when the signal exceeds the noise for 5 consecutive years for the first time. The EoC is defined as CO₂ 240 241 concentration difference (Δ [CO₂]) between the time of emergence and the year 1901 (see Fig. 1 for example). We also test the sensitivity of the arbitrary choice of 5 years 242 243 in the calculation of EoC and present results also for n (n = 3, 5, 7, 9) years (Fig. S4). For analyzing the freeze-CO₂ experiment we use the same approach to derive the 244 245 EoC. The only difference is that we set the initial year of keeping CO₂ constant to 1988 instead of 1901. 246



247

Fig. 1 Illustration of detection of emergence of the elevated CO₂ effects (EoC). The solid lines depict the time series of annual mean GPP for one example site in QUINCY (80.75° W, 37.75° N, temperate broadleaved summer green tree). Black color denotes the time series from the transient-CO₂ experiment, while gray color denotes the time series from the constant-CO₂ experiment (for details see section 2.1.2.2). The shaded area represents the standard error of the linear regression slope

254 (black or gray dashed line). The vertical dashed red line indicates the earliest time at

which the black and gray trends deviate significantly. EoC describes the value of

256 Δ [CO₂] needed to reach this point.

257 Table 1 Variables and metrics analyzed for the emergence of the elevated CO₂

258 effects.

Variable or metric	Abbreviation
Gross primary production	GPP
Transpiration	Tr
Normalized transpiration per leaf area (Tr/LAI)	Tr _{norm}
Leaf area index	LAI
Net primary production	NPP
Biomass	
Evaporation	
Interception loss	
Root-zone soil moisture	
Light-use efficiency (GPP/Absorbed photosynthetically active radiation (APAR))	LUE
Underlying water-use efficiency ($GPP \times \sqrt{VPD}/Tr$)	uWUE
Normalized canopy conductance (canopy conductance $(gc)/(VPD \times LAI)$	gc _{norm}
95 th percentile of daily GPP values in each year	GPP ⁹⁵
95 th percentile of daily Tr _{norm} values in each year	Tr _{norm} ⁹⁵

260 In this study, we mainly focus on the CO₂-induced change on annual average values 261 of the relevant variables and metrics for all sites. Based on existing knowledge, we select variables or metrics (Table 1) that are hypothesized to be most sensitive to 262 263 eCO₂ (Drake et al., 1997; Novick et al., 2016; Knauer et al., 2017; Ueyama et al., 2020; Migliavacca et al., 2021) to investigate the first manifestations of eCO₂. In addition, to 264 265 analyze the variation of the CO₂ fertilization effect at different time scales, we apply the same detecting method at specific times-of-day in each year (e.g., 1 May, 8am) 266 instead of annual means, to derive the EoC at seasonal and diurnal scale for 267 268 representative sites from each vegetation classes (Table S1).

269 2.2.3 Variable importance determined with random forest analysis

270 After determining EoC for each site-level simulation, we obtain the respective spatial 271 distribution of EoC across sites. We evaluate the relative contribution from all drivers 272 to the spatial variability in EoC by applying SHapley Additive exPlanation (SHAP) 273 value analysis based on the random forest (RF) model. First, we train the RF model 274 (scikit-learn RandomForestRegressor API in Python, Pedregosa et al., 2011) to 275 predict the previously computed EoC patterns across sites using site-specific longterm (1901-2018) means of climate factors (i.e., temperature, precipitation, soil 276 277 moisture, VPD, aridity index (evapotranspiration/precipitation)) and vegetation related factors (i.e. GPP, LAI, canopy height, growing season length) as predictors (Fig. S10). 278 279 The long-term mean values are computed over the entire simulation period from the 280 transient-CO₂ experiment. The out-of-bag (oob) score estimates the accuracy of the 281 prediction from the RF model as compared with the actual EoC values, where a higher

value (the maximum score equals 1) represents a better performance of the model.
Finally, we use the module "SHAP TreeExplainer" from the software package shap in
Python (Lundberg and Lee, 2017; Lundberg et al., 2020) to examine the influence of
all the involved predictors. The average of the absolute SHAP values for each predictor
indicates its impact on the target variable (i.e., spatial variability of EoC).

287 2.3 Comparison with simulations from Earth system models288 (CMIP6)

In addition, we perform the EoC analysis for GPP and Tr_{norm} using simulations from 7 289 290 Earth system models (ESMs) from the most recent Coupled Model Intercomparison 291 Project (CMIP6). We use simulation output of the CMIP6 experiments 1pctCO2 and 292 1pctCO2-rad. In both experiments, the CO₂ concentration increases gradually at a rate 293 of 1 percent per year until quadrupling, starting at the pre-industrial equilibrium state 294 (Meehl et al., 2014). The fully coupled model setup is used in the 1pctCO2 experiment, 295 while for the 1pctCO2-rad experiment the CO2 concentration is kept at the pre-296 industrial level for the carbon cycle and the increasing CO₂ has only a radiative effect 297 (i.e., CO₂-induced climatic changes, Jones et al., 2016). Therefore, the 1pctCO2 298 experiment is comparable to our transient-CO₂ experiment, and the 1pctCO2-rad experiment is comparable to our constant-CO₂ experiment, although the QUINCY 299 300 simulations follow the observed CO₂ concentration for the last 120 years. EoC is 301 calculated by applying the same detection method as described in section 2.2.2. To 302 obtain comparability to the EoC results based on the QUINCY simulations, we select 303 cells in gridded CMIP6 output which correspond to the locations of simulated sites with QUINCY. Further, we only consider the CMIP6 time series from the year 1850 until 304 the doubling of the atmospheric CO₂ concentration, i.e., roughly 560 ppm. The ESMs 305

306 used in this study are (1) Beijing Climate Center (BCC) BCC-CSM2-MR, (2) Institut Pierre Simon Laplace (IPSL) IPSL-CM6A-LR, (3) Centre National de Recherches 307 308 Météorologiques (CNRM) CNRM-ESM2-1, (4) United Kingdom (UK) UKESM1-0-LL, 309 (5) Canadian Centre for Climate Modelling and Analysis (CCCma) CanESM5, (6) Meteorological Research Institute of the Japan Meteorological Agency (MRI) MRI-310 311 ESM2-0, (7) Max Planck Institute for Meteorology (MPI) MPI-ESM1.2-LR. More details on the used CMIP6 ESMs can be found in (Arora et al., 2020). Due to missing 312 313 respective output, the analysis for normalized transpiration (Tr_{norm}) only involves the 314 first 4 models in the CMIP6 archive.

315 3 Results and Discussion

316 3.1 The effect of elevated CO₂ on gross primary production

317 Our analysis based on model simulation experiments indicates that eCO₂ generally 318 increases GPP. This increase in GPP differs in magnitude and interannual variability across climate and vegetation types (Fig. 2). The trend of increasing GPP over 118 319 320 years is clearly visible in all forested sites and less clear at grassland sites due to high year-to-year variability in GPP. In comparison to the forested sites, the variability in 321 322 GPP is considerably higher at grassland sites, because grass-dominated ecosystems are more sensitive to climate variability partly related to shallower roots (Kulmatiski et 323 324 al., 2020; Miguez-Macho and Fan, 2021) and less regulated by stomatal closure 325 (Konings et al., 2017). Grasslands are also predominantly located in semi-arid regions, in which interannual variability of precipitation is large, and therefore has a larger 326 imprint on GPP that it would have in mesic ecosystems with lower precipitation 327

interannual variability (Maurer et al., 2020). The grassland sites that are located in
relatively cold regions show less variability and more clear trends in GPP in contrast
to grassland sites located in warmer (and drier) regions.

331 Overall, the results show that the CO₂ fertilization effect is strong where vegetation productivity is not strongly limited by energy or water availability. Subdividing the 332 333 temperature classes further based on the amount of annual precipitation, we are able 334 to assess the role of water availability in controlling the variability in GPP (Fig. S2). 335 Sites located in relatively warm and wet regions in the Temperate and the Boreal 336 Forest vegetation class (Fig. S2 b and c) also exhibit the sharpest increase in GPP. This is probably related to the temperature-dependent response of photosynthetic rate 337 338 of CO₂ uptake through the kinetics of the Rubisco enzyme (Long, 1991; Hickler et al., 339 2008; Baig et al., 2015). However, the difference of increase in LUE across 340 temperature and precipitation classes are not apparent compared to where we find the 341 sharp increase in GPP, especially in the Temperate Forest vegetation class (Fig. S1 b). The increased carbon assimilation due to rising CO₂ leads to a build-up of more 342 biomass, some of which is allocated to increased leaf growth resulting in an extension 343 344 of the leaf area (Winkler et al., 2021). Canopies with higher LAI are more available for 345 light interception and therefore it leads to enhancement of vegetation productivity. In 346 temperate forest, the enhancement of GPP due to eCO₂ is the combination of 347 increased both LAI and photosynthetic efficiency (Norby et al., 2005; McCarthy et al., 2006). 348



Fig. 2 Differences in annual average GPP between the transient-CO₂ and the constant-CO₂ experiments across climate and vegetation classes. All global sites (339 sites) are first grouped by vegetation type (a-d, Table S1) and then by long-term mean temperature using quantiles within each group (cold in blue: ≤ 0.33 ; warm in orange: 0.33 - 0.66; hot in purple: ≥ 0.66). The shaded area depicts standard deviation around the multi-sites mean value (solid lines).

349

356 3.2 The effect of elevated CO₂ on transpiration per leaf area

357 Decreased transpiration (Tr) due to down-regulated gas exchange with the 358 atmosphere at the leaf level can be offset by an extension in leaf area at the canopy 359 level. The simulated Tr exhibits both increasing and decreasing trends in response to 360 eCO_2 . To account for that, we normalized Tr by LAI which is denoted by Tr_{norm}. Tr_{norm} 361 thus represents the transpiration per leaf area. 362 As expected, we find consistently decreasing Tr_{norm} across all vegetation types and temperature classes (Fig. 3). Similar to the result in section 3.1 (Fig. 2), the variability 363 in Tr_{norm} is high in grasslands. In contrast to GPP, Tr_{norm} responds to eCO₂ strongly 364 where temperature and precipitation are relatively low except for tropical forest sites 365 (Fig. S2). Barton et al. (2012) suggested that the ratio of net photosynthesis to 366 transpiration increases in proportion to the increase in atmospheric CO₂ concentration. 367 368 They further demonstrated that stomatal conductance responds to eCO₂ not as strongly as the photosynthesis apparatus. At the leaf level, the decreased stomatal 369 370 conductance is likely to result in the increase of leaf skin temperature (Leakey et al., 371 2009), which demands higher transpiration. However, the direct relationship between ambient temperature and eCO₂ effect on stomatal regulation is still ambiguous 372 373 (Medlyn et al., 2001; Barton et al., 2012).



374

Fig. 3 Differences in annual average Tr_{norm} between the transient-CO₂ and the constant-CO₂ experiments across climate and vegetation classes. All global sites

377 (339 sites) are first grouped by vegetation type (a-d, Table S1) and then by 378 temperature using quantiles (cold in blue: ≤ 0.33 ; warm in orange: 0.33 - 0.66; hot in 379 purple: ≥ 0.66). The shaded area depicts standard deviation around the multi-sites 380 mean value (solid lines).

381 3.3 Emergence of the elevated CO₂ effects (EoC) in GPP

382 and Tr_{norm}

383 A lower EoC indicates a detection of eCO₂ effects earlier in the analyzed time period and thus a stronger response in the target variable to the eCO₂ effects compared to 384 its background or natural variability. Our results show that the eCO₂ effect in GPP is 385 strongest in the tropical forests. 44 sites exhibit an EoC of less than 20 ppm (Fig. 4). 386 This means that a change in atmospheric CO₂ of 20 ppm is sufficient to detect the CO₂ 387 fertilization effect in the GPP time series for those sites. The forested northern mid-388 and high-latitudes also exhibit significant changes in GPP, which, however, is only 389 390 detectable at much higher Δ [CO₂] (consistent with Schimel et al., 2015). GPP in arid 391 regions is highly variable due to the high sensitivity towards intermittent water availability, and this prevents a detection of the CO₂ fertilization effect. The effect of 392 eCO₂ on GPP further rarely emerges in regions dominated by C4 grasses, most likely 393 because they are less responsive to eCO₂ due to their different photosynthetic 394 pathway (Leakey et al., 2009). Also, evidence from FACE experiments suggests that 395 396 trees exhibit the greatest response to eCO₂ compared to C3 and C4 grasses 397 (Ainsworth and Long, 2005). The magnitude of plants' responses to eCO₂ comes down to the variations of photosynthetic capacity, which is indicated by the maximum rate of 398

RuBisCO carboxylase activity (Vc_{max}) and the maximum rate of photosynthetic electron transport (J_{max}; Long, 1991). We find a similar pattern of distribution for EoC in LUE (Fig. S5) with EoC in GPP, which could support the physiological effect of eCO_2 on GPP rather than structural change, namely the change of LAI.

403 EoC in Tr_{norm} is substantially higher compared to GPP, i.e., the signal emerges only at considerably higher Δ [CO₂]. Further, the global spatial pattern of EoC is more 404 homogeneous for Tr_{norm} than for GPP. Several equatorial sites exhibit a relatively low 405 406 EoC (some of them even less than 40 ppm), but for most sites (123 in 152 detected sites) the signal only emerges at Δ [CO₂] > 70 ppm or not at all. Especially at sites in 407 408 arid and semi-arid regions, no significant effect of eCO₂ can be detected, even though 409 a strong response in water-use efficiency is expected to occur in these water-limited 410 ecosystems (Medlyn et al., 2001). In the QUINCY model, canopy conductance and transpiration does not scale linearly with LAI at canopy level. So, the Tr_{norm} could still 411 412 be affected by increasing LAI to some extent. Next to this, transpiration can be affected 413 by other factors which may overshadow the role of stomatal conductance. For 414 example, transpiration is affected by incoming radiation particularly when vegetation is strongly decoupled with the boundary layer, i.e., a low exchange rate between 415 416 vegetation and atmosphere (Jarvis, 1985; De Kauwe et al., 2017). Due to the limited 417 representation of the coupling between vegetation and the boundary layer in models, 418 the reduced transpiration flux at the leaf-level might not scale to the canopy-level. 419 The freeze-CO₂ experiment (see section 2.1.2.2) reveals if the results are still

informative for climate change in recent years (1988-2018). Due to the limited length
of the time period, there are only a few sites where the eCO₂ effect on GPP can be

detected (Fig. S6). Nevertheless, as the result shown in Fig. 4a, the signal first
emerges in the tropical regions, with a rather low EoC of around 20 ppm. Furthermore,
the EoC for tropical GPP is consistent between two time periods (1901-2018 and 19882018). This encourages future study of the CO₂ fertilization effect in recent years.



427

Fig. 4 Global distribution of emergence of the elevated CO_2 effects (EoC) in (a) GPP and (b) Tr_{norm}. Bright color indicates an earlier detection (lower EoC), and dark color indicates a later detection (higher EoC). Non-colored points indicate sites where the elevated CO_2 does not translate into significant changes in GPP or Tr_{norm} within the historical time period.

433 3.4 Seasonal and diurnal variation of EoC in GPP

434 We find plants respond differently to the effects of eCO₂ across different climate zones 435 and vegetation types, but also in different seasons and times of the day. For example, 436 EoC in GPP is lower in summer than in other seasons at sites in the temperate and 437 boreal forests (Fig. S7 a, d), which is obviously driven by favorable growing conditions. However, this is not always the case at the diurnal time scale where lowest EoC are 438 439 partly found at other times than noon. For the sites in temperate and boreal forests, 440 the strong signal already emerges early in the morning on some days during summer. 441 It could be related to the increased aridity at midday. The excessive atmospheric 442 moisture demand at high temperature results in the midday depression of carbon uptake, and thus stomatal limitation, which can be simulated by the model. Unlike for 443 444 the boreal forest site, at the tropical forest site (Fig. S7 b), the plant response to eCO₂ 445 can be detected for any time during the daytime and in all seasons. Although the effect of eCO₂ on GPP cannot be detected at grass sites at the annual scale, we can detect 446

it in the early growing season, albeit only at very high Δ [CO₂] > ~100 ppm (Fig. 3, Fig.

448 S7 c). The EoC in Tr_{norm} however is not detectable at any point of the the seasonal 449 and diurnal cycle, probably related to high variability of the meteorological conditions, which can be reduced to some extent by the aggregation to annual values. In the 450 future, researchers may explore the drivers of the variation across diurnal and 451 452 seasonal scales. Furthermore, we find the EoC in GPP is lower at some points of the seasonal and diurnal cycle than EoC in GPP at the annual scale (Fig. S7). This 453 454 motivates future study of eCO₂ effects in observations at the seasonal and diurnal time 455 scale.

456 3.5 EoC in secondary variables triggered by plant physiological 457 effects

Changes in GPP and Tr_{norm} triggered by the effects of eCO₂ can cascade into 458 459 secondary state and process variables of the carbon (e.g., LAI, biomass, NPP) and 460 water cycles (e.g., evaporation, interception loss, soil moisture). The EoC in LAI and 461 biomass are generally low (Fig. S8 a, b), even lower than in the case of GPP. Note that this does not mean that LAI responds more strongly to CO₂ increases than GPP, 462 463 but rather this finding illustrates the effect of the internal variabilities of each variable 464 on our results where LAI and biomass as state variables are less influenced by shortterm and interannual hydro-meteorological variations and therefore its variation has a 465 466 substantially lower standard deviation. The higher signal-to-noise ratio enables the detection of the eCO₂ effects already early in the time series where CO₂ has not yet 467 468 increased much. Additionally, there is a non-linear relationship between GPP and LAI when LAI is high. GPP tends to saturate with high LAI due to clumping and the 469 470 increase of shaded leaves in the canopy (Street et al., 2007; Chen et al., 2012; Lee et 471 al., 2019). However, except for the eCO₂ effect, different carbon allocation representations in models also affect the prediction for where the additionally 472 assimilated carbon goes (Kauwe et al., 2014). Further, the modeled carbon pathways 473 474 do not always agree with observational evidence from elevated CO₂ experiments (Norby and Zak, 2011). EoC in NPP shows a similar spatial pattern compared to EoC 475 476 in GPP, only the EoC is overall higher due to the added variability from autotrophic 477 respiration (Fig. S8 c).

The natural variability of process and state variables in the water cycle (e.g., evaporation, interception, root-zone soil moisture) is substantially higher than for the

480 carbon cycle variables. The increasing LAI could provide more shading area, resulting 481 in a cooling of the surface soil layer. The evaporation from bare soil decreases as a 482 consequence of this reduced radiative energy input. Consequently, the EoC in 483 evaporation can be detected in sites located mainly in tropical regions and mid-latitude 484 regions (Fig. S8 d). Evaporation from rainfall interception is expected to remarkably 485 increase due to the substantial increase in LAI. However, the magnitude of increased interception loss does not stand out from the year-to-year variability controlled by 486 stochastic precipitation events. Also, the root-zone soil moisture does not exhibit a 487 clear response to eCO₂. This is related to the complex and interacting effects on 488 related water fluxes such as soil evaporation, transpiration, interception loss and 489 490 runoff. The interannual variability in precipitation likely also overshadows the subtle 491 changes in soil moisture in response to the effects of eCO₂ (De Kauwe et al., 2021).

492 3.6 First manifestations of elevated CO₂

493 In this section we compare the EoC across several variables and metrics (Table 1) 494 related to the carbon and water cycles. These variables and metrics include the 495 underlying water-use efficiency (uWUE), the light-use efficiency (LUE), the normalized canopy conductance (gcnorm), LAI and the 95th percentiles of GPP (GPP⁹⁵) and Trnorm 496 (Tr_{norm⁹⁵}). EoC is lowest for GPP⁹⁵ and LAI for most sites (167 in 214 detected sites; 497 Fig. 5). We consider the 95th percentile of daily GPP values in each year (GPP⁹⁵) to 498 be representative of the maximum capacity of vegetation productivity, which is less 499 affected by day-to-day weather variability. EoC in GPP⁹⁵ is significantly lower since 500 much of the variability is removed compared to annual mean GPP. EoC in GPP⁹⁵ and 501 LAI are comparable in the vegetation classes Tropical and Boreal Forests (Fig. S9). 502 503 However, EoC in LAI in the Temperate Forests and Grass vegetation classes tends to 504 be considerably higher. Probably, this is due to the different fraction of carbon 505 allocated to foliage versus other plant components across vegetation types (De Kauwe 506 et al., 2014).

EoC in LUE emerges first for sites located in the high latitudinal regions, where plant growth is considered to be energy-limited. EoC in WUE emerges first for sites in arid regions, where plant growth is limited by water availability. Compared to variables related to the carbon cycle (e.g., GPP, GPP⁹⁵, LAI), variables related to the water cycle (e.g., gc_{norm} , Tr_{norm} , Tr_{norm} ⁹⁵) show weaker responses to the physiological effects of eCO₂.





523 3.7 Explaining the spatial variability of EoC in GPP and

524 Tr_{norm}

525 The ecosystem responses to eCO₂ are complex and modulated by several concurrent effects. All drivers considered to explain the spatial variability of EoC are calculated as 526 527 long-term mean values (see section 2.2.3). We find that the spatial variability of EoC in GPP and Tr_{norm} between sites is mainly explained by varying levels of mean LAI and 528 mean GPP, respectively (Fig. S10). The higher the mean LAI (or mean GPP), the less 529 530 Δ [CO₂] is required such that the physiological effects of eCO₂ emerge in GPP, 531 respectively, Tr_{norm} fluxes. Next, we compare these relationships based on the QUINCY model with output from similar simulations of Earth system models conducted 532 533 in CMIP6 (see section 2.3). Most CMIP6 models qualitatively agree with the QUINCY 534 results, i.e., the negative relationship between spatial EoC in GPP and LAI, and the 535 negative relationship between spatial EoC in Tr_{norm} and GPP (Fig. 6). Four models in 536 CMIP6 (Fig. S11 (a)(e)(f)(g)) agree with QUINCY (Fig. S11 (h)), while the other three of them do not show a negative relationship between EoC in GPP and the long-term 537 538 mean LAI. Also, there are considerable differences between the magnitude of EoC across the models as well as the strength of the relationships vary among the 539 540 individual models in CMIP6 (Fig. S11, Fig. S12). We note, however, that this direct 541 comparison between the QUINCY and the CMIP6 simulations is limited due to the 542 conceptually different setup of the analysed simulations. Furthermore, in contrast to the QUINCY model, which is an offline terrestrial biosphere point model, the CMIP6 543 544 ensemble comprises fully coupled Earth system models, which represent a gridded and coupled land-atmosphere system. Despite these conceptual differences, the 545

546 overall agreement between the QUINCY and CMIP6 models illustrated in Fig. 6 547 corroborates our findings based on the QUINCY model formulation.





Fig. 6 EoC in QUINCY versus coupled Earth system models. Spatially varying EoC is plotted against the predictor that explains most of its spatial variability according to the SHAP value analysis illustrated in Fig. S10. The relationship of (a) EoC in GPP is plotted against respective LAI of each model; and (b) EoC in Tr_{norm} is plotted against respective baseline GPP from each model.

554 4 Conclusion

We evaluate the plant physiological effects of elevated CO_2 (e CO_2) on the landatmosphere exchange of carbon and water. Increasing atmospheric CO_2 stimulates plant carbon assimilation and reduces stomatal conductance, which both may result in a potential increase in ecosystem productivity and also affect ecosystem transpiration. Analyzing approximately the last 120 years simulated by the terrestrial biosphere model QUINCY, we assess how strong the increase in CO_2 needs to be such that the effects of eCO₂ surpass the noise and effects induced by short and longterm meteorological conditions.

We find that the eCO_2 effects on GPP can be earlier detected compared with transpiration (Tr). The eCO_2 effects on GPP are different across climate and biomes, whereas eCO_2 effects on normalized transpiration (Tr_{norm}) exhibit less spatial variability. The eCO_2 effects on GPP are detectable at relatively low CO_2 increase

567 (Δ [CO₂] ~ 20 ppm) in regions where vegetation productivity is not strongly constrained

568 by climatic conditions, i.e., water- or temperature-limited plant growth. Carbon 569 assimilation and carbon pools show stronger responses to eCO₂ across sites while we 570 do not find a widespread strong eCO₂ effect in variables describing the water cycle. 571 The transpiration at canopy level is regulated by the reduced stomatal conductance 572 and meanwhile, the increasing LAI in response to eCO₂. These two opposing effects 573 appear to be cancelled each other out at ecosystem level and longer time scales, resulting in an insignificant eCO₂ effect on transpiration and other water cycle variables 574 575 (e.g., evaporation, interception loss and soil moisture) which are affected by the 576 response of Tr. While mostly GPP and LAI are the first variables to exhibit detectable eCO₂ effects, in northern high-latitude regions where vegetation growth is limited by 577 radiation, light-use efficiency responds to eCO₂ first among all the other variables, and 578 579 the eCO₂ effects on water-use efficiency emerges first in some sites located in semi-580 arid regions.

581 Climate variations can partly explain the spatial heterogeneity of the plant 582 physiological effects of eCO_2 . The strongest response of GPP or Tr_{norm} to eCO_2 occurs 583 dominantly where GPP is not limited by either temperature or precipitation (e.g., sites 584 in tropical regions). The weakest response of GPP or Tr_{norm} occurs in arid regions

585 (e.g., grassland sites), where the high variability overshadows the eCO_2 effect. In 586 addition to climate factors, eCO₂-induced plant physiological effects are amplified where vegetation productivity is already high. We find the long-term mean LAI is the 587 588 dominant driver of spatial variability of the eCO₂ effect on GPP, whereas the long-term mean GPP is the dominant driver of spatial variability of the eCO₂ effect on Tr_{norm}. 589 590 Despite the different model structures and simulation setups, the CMIP6 models 591 essentially are consistent with the insights gained from the QUINCY model about what 592 drives spatial variance in the emergence of the eCO₂ effects. Overall, our results thus 593 suggest that high-LAI regions, e.g., tree-dominated ecosystems are more sensitive to the eCO₂ effect than low-LAI, e.g., grass-dominated ecosystems. 594

595 Models have the advantage for hypothesis testing by conducting idealized 596 experiments. Using these experiments, we determine when and where we expect to 597 detect the eCO₂ effects according to our theoretical understanding formulated in the 598 models. This knowledge provides a first step towards assessing long-term changes 599 and trends in carbon and water flux observations using eddy covariance 600 measurements (Baldocchi et al., 2001). In a future study, we will apply this 601 methodology to analyze whether eCO₂ effects can already be detected in the time 602 series of long-term measurement campaigns of land-atmosphere exchange fluxes, 603 focusing on the regions and time scales of eCO₂ effects spotlighted in this precursory 604 study. Overall, the model-based analyses presented here, along with the ongoing observational study focused on the detection and potential quantification of eCO₂ 605 effects, are critical and have long been called for in order to provide robust 606 607 assessments of how the system will continue to change as CO₂ continues to rise.

608 Acknowledgements

609 Chunhui Zhan is supported by the International Max Planck Research School (IMPRS). 610 Markus Reichstein and Alexander J. Winkler acknowledge support by the European Research 611 Council (ERC) Synergy Grant "Understanding and Modelling the Earth System with Machine 612 Learning (USMILE)" under the Horizon 2020 research and innovation programme (Grant 613 agreement No. 855187). René Orth is supported by the German Research Foundation (Emmy 614 Noether grant number 391059971). Sönke Zaehle and Jan Engel were supported by the 615 European Research Council (ERC) under the European Union's Horizon 2020 research and 616 innovation programme (QUINCY; grant no. 647204). Chunhui Zhan thanks Silvia Caldararu 617 and Lin Yu for their support in working with the QUINCY model.

618 Author contributions

619 Chunhui Zhan, Rene Orth and Alexander J. Winkler jointly designed this study. Mirco 620 Migliavacca, Sönke Zaehle and Markus Reichstein contributed to ideas and experimental 621 design. Alexander J. Winkler preprocessed the CMIP6 model simulations. Jan Engel 622 contributed to technical assistance for the QUINCY model. All authors contributed to the 623 writing of the paper, the discussion and interpretation of the results.

624 Competing interests

625 The authors declare that there are no competing interests.

626 References

Ainsworth, E.A., Long, S.P., 2005. What have we learned from 15 years of free-air CO2
 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis,

629 canopy properties and plant production to rising CO2. New Phytol. 165, 351–372.

630 https://doi.org/10.1111/j.1469-8137.2004.01224.x

- Ainsworth, E.A., Rogers, A., 2007. The response of photosynthesis and stomatal
 conductance to rising [CO2]: mechanisms and environmental interactions. Plant Cell
 Environ. 30, 258–270. https://doi.org/10.1111/j.1365-3040.2007.01641.x
- Arora, V.K., Katavouta, A., Williams, R.G., Jones, C.D., Brovkin, V., Friedlingstein, P.,
- 635 Schwinger, J., Bopp, L., Boucher, O., Cadule, P., Chamberlain, M.A., Christian, J.R.,
- 636 Delire, C., Fisher, R.A., Hajima, T., Ilyina, T., Joetzjer, E., Kawamiya, M., Koven,
- 637 C.D., Krasting, J.P., Law, R.M., Lawrence, D.M., Lenton, A., Lindsay, K., Pongratz,
- J., Raddatz, T., Séférian, R., Tachiiri, K., Tjiputra, J.F., Wiltshire, A., Wu, T., Ziehn,
- T., 2020. Carbon–concentration and carbon–climate feedbacks in CMIP6 models and
- their comparison to CMIP5 models. Biogeosciences 17, 4173–4222.
- 641 https://doi.org/10.5194/bg-17-4173-2020
- Baig, S., Medlyn, B.E., Mercado, L.M., Zaehle, S., 2015. Does the growth response of
 woody plants to elevated CO2 increase with temperature? A model-oriented metaanalysis. Glob. Change Biol. 21, 4303–4319. https://doi.org/10.1111/gcb.12962
- Baldocchi, D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer,
- 646 C., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X., Malhi,
- 647 Y., Meyers, T., Munger, W., Oechel, W., U, K.T.P., Pilegaard, K., Schmid, H.P.,
- 648 Valentini, R., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2001. FLUXNET: A New
- Tool to Study the Temporal and Spatial Variability of Ecosystem-Scale Carbon
- 650 Dioxide, Water Vapor, and Energy Flux Densities. Bull. Am. Meteorol. Soc. 82, 2415–
- 651 2434. https://doi.org/10.1175/1520-0477(2001)082<2415:FANTTS>2.3.CO;2
- Barton, C.V.M., Duursma, R.A., Medlyn, B.E., Ellsworth, D.S., Eamus, D., Tissue, D.T.,
- Adams, M.A., Conroy, J., Crous, K.Y., Liberloo, M., Löw, M., Linder, S., McMurtrie,
- 654 R.E., 2012. Effects of elevated atmospheric [CO2] on instantaneous transpiration
- efficiency at leaf and canopy scales in Eucalyptus saligna. Glob. Change Biol. 18,
- 656 585–595. https://doi.org/10.1111/j.1365-2486.2011.02526.x

- Bastos, A., Ciais, P., Friedlingstein, P., Sitch, S., Pongratz, J., Fan, L., Wigneron, J.P.,
- 658 Weber, U., Reichstein, M., Fu, Z., Anthoni, P., Arneth, A., Haverd, V., Jain, A.K.,
- Joetzjer, E., Knauer, J., Lienert, S., Loughran, T., McGuire, P.C., Tian, H., Viovy, N.,
- 660 Zaehle, S., 2020. Direct and seasonal legacy effects of the 2018 heat wave and
- drought on European ecosystem productivity. Sci. Adv.
- 662 https://doi.org/10.1126/sciadv.aba2724
- 663 Chen, J.M., Mo, G., Pisek, J., Liu, J., Deng, F., Ishizawa, M., Chan, D., 2012. Effects of
 664 foliage clumping on the estimation of global terrestrial gross primary productivity.

Glob. Biogeochem. Cycles 26. https://doi.org/10.1029/2010GB003996

- 666 De Kauwe, M.G., Medlyn, B.E., Knauer, J., Williams, C.A., 2017. Ideas and perspectives:
- how coupled is the vegetation to the boundary layer? Biogeosciences 14, 4435–
 4453. https://doi.org/10.5194/bg-14-4435-2017
- De Kauwe, M.G., Medlyn, B.E., Tissue, D.T., 2021. To what extent can rising [CO2]
 ameliorate plant drought stress? New Phytol. 231, 2118–2124.

671 https://doi.org/10.1111/nph.17540

- 672 Drake, B.G., Gonzàlez-Meler, M.A., Long, S.P., 1997. MORE EFFICIENT PLANTS: A
- 673 Consequence of Rising Atmospheric CO2? Annu. Rev. Plant Physiol. Plant Mol. Biol.
- 674 48, 609–639. https://doi.org/10.1146/annurev.arplant.48.1.609
- 675 Fernández-Martínez, M., Vicca, S., Janssens, I.A., Ciais, P., Obersteiner, M., Bartrons, M.,
- 676 Sardans, J., Verger, A., Canadell, J.G., Chevallier, F., Wang, X., Bernhofer, C.,
- 677 Curtis, P.S., Gianelle, D., Grünwald, T., Heinesch, B., Ibrom, A., Knohl, A., Laurila,
- T., Law, B.E., Limousin, J.M., Longdoz, B., Loustau, D., Mammarella, I., Matteucci,
- G., Monson, R.K., Montagnani, L., Moors, E.J., Munger, J.W., Papale, D., Piao, S.L.,
- 680 Peñuelas, J., 2017. Atmospheric deposition, CO 2, and change in the land carbon
- 681 sink. Sci. Rep. 7, 9632. https://doi.org/10.1038/s41598-017-08755-8
- 682 Friedlingstein, P., Jones, M.W., O'Sullivan, M., Andrew, R.M., Hauck, J., Peters, G.P.,
- 683 Peters, W., Pongratz, J., Sitch, S., Le Quéré, C., Bakker, D.C.E., Canadell, J.G.,
- 684 Ciais, P., Jackson, R.B., Anthoni, P., Barbero, L., Bastos, A., Bastrikov, V., Becker,

685	M., Bopp, L., Buitenhuis, E., Chandra, N., Chevallier, F., Chini, L.P., Currie, K.I.,
686	Feely, R.A., Gehlen, M., Gilfillan, D., Gkritzalis, T., Goll, D.S., Gruber, N., Gutekunst,
687	S., Harris, I., Haverd, V., Houghton, R.A., Hurtt, G., Ilyina, T., Jain, A.K., Joetzjer, E.,
688	Kaplan, J.O., Kato, E., Klein Goldewijk, K., Korsbakken, J.I., Landschützer, P.,
689	Lauvset, S.K., Lefèvre, N., Lenton, A., Lienert, S., Lombardozzi, D., Marland, G.,
690	McGuire, P.C., Melton, J.R., Metzl, N., Munro, D.R., Nabel, J.E.M.S., Nakaoka, SI.,
691	Neill, C., Omar, A.M., Ono, T., Peregon, A., Pierrot, D., Poulter, B., Rehder, G.,
692	Resplandy, L., Robertson, E., Rödenbeck, C., Séférian, R., Schwinger, J., Smith, N.,
693	Tans, P.P., Tian, H., Tilbrook, B., Tubiello, F.N., van der Werf, G.R., Wiltshire, A.J.,
694	Zaehle, S., 2019. Global Carbon Budget 2019. Earth Syst. Sci. Data 11, 1783–1838.
695	https://doi.org/10.5194/essd-11-1783-2019
696	Gedney, N., Cox, P.M., Betts, R.A., Boucher, O., Huntingford, C., Stott, P.A., 2006.
697	Detection of a direct carbon dioxide effect in continental river runoff records. Nature
698	439, 835–838. https://doi.org/10.1038/nature04504
699	Gentine, P., Green, J.K., Guérin, M., Humphrey, V., Seneviratne, S.I., Zhang, Y., Zhou, S.,
700	2019. Coupling between the terrestrial carbon and water cycles—a review. Environ.
701	Res. Lett. 14, 083003. https://doi.org/10.1088/1748-9326/ab22d6
702	Good, S.P., Noone, D., Bowen, G., 2015. Hydrologic connectivity constrains partitioning of
703	global terrestrial water fluxes. Science 349, 175–177.
704	https://doi.org/10.1126/science.aaa5931
705	Hengl, T., Jesus, J.M. de, Heuvelink, G.B.M., Gonzalez, M.R., Kilibarda, M., Blagotić, A.,
706	Shangguan, W., Wright, M.N., Geng, X., Bauer-Marschallinger, B., Guevara, M.A.,
707	Vargas, R., MacMillan, R.A., Batjes, N.H., Leenaars, J.G.B., Ribeiro, E., Wheeler, I.,
708	Mantel, S., Kempen, B., 2017. SoilGrids250m: Global gridded soil information based
709	on machine learning. PLOS ONE 12, e0169748.
710	https://doi.org/10.1371/journal.pone.0169748
711	Hickler, T., Smith, B., Prentice, I.C., Mjöfors, K., Miller, P., Arneth, A., Sykes, M.T., 2008.

712 CO2 fertilization in temperate FACE experiments not representative of boreal and

713 tropical forests. Glob. Change Biol. 14, 1531–1542. https://doi.org/10.1111/j.1365714 2486.2008.01598.x

- Jarvis, P.G., 1985. Transpiration and assimilation of tree and agricultural crops: the "omega
 factor." Attrib. Trees Crop Plants Ed. MGR Cannell JE Jackson.
- Jones, C.D., Arora, V., Friedlingstein, P., Bopp, L., Brovkin, V., Dunne, J., Graven, H.,
- 718 Hoffman, F., Ilyina, T., John, J.G., Jung, M., Kawamiya, M., Koven, C., Pongratz, J.,
- 719 Raddatz, T., Randerson, J.T., Zaehle, S., 2016. C4MIP & ndash; The Coupled
- 720 Climate–Carbon Cycle Model Intercomparison Project: experimental protocol for
- 721 CMIP6. Geosci. Model Dev. 9, 2853–2880. https://doi.org/10.5194/gmd-9-2853-2016
- Kauwe, M.G.D., Medlyn, B.E., Zaehle, S., Walker, A.P., Dietze, M.C., Wang, Y.-P., Luo, Y.,
- Jain, A.K., El-Masri, B., Hickler, T., Wårlind, D., Weng, E., Parton, W.J., Thornton,
- 724 P.E., Wang, S., Prentice, I.C., Asao, S., Smith, B., McCarthy, H.R., Iversen, C.M.,
- Hanson, P.J., Warren, J.M., Oren, R., Norby, R.J., 2014. Where does the carbon go?
- A model–data intercomparison of vegetation carbon allocation and turnover
- 727 processes at two temperate forest free-air CO2 enrichment sites. New Phytol. 203,
- 728 883–899. https://doi.org/10.1111/nph.12847
- Keenan, T.F., Hollinger, D.Y., Bohrer, G., Dragoni, D., Munger, J.W., Schmid, H.P.,
- 730 Richardson, A.D., 2013. Increase in forest water-use efficiency as atmospheric
- carbon dioxide concentrations rise. Nature 499, 324–327.
- 732 https://doi.org/10.1038/nature12291
- 733 Knauer, J., Zaehle, S., Reichstein, M., Medlyn, B.E., Forkel, M., Hagemann, S., Werner, C.,
- 734 2017. The response of ecosystem water-use efficiency to rising atmospheric CO ₂
- 735 concentrations: sensitivity and large-scale biogeochemical implications. New Phytol.
- 736 213, 1654–1666. https://doi.org/10.1111/nph.14288
- 737 Konings, A.G., Williams, A.P., Gentine, P., 2017. Sensitivity of grassland productivity to
- aridity controlled by stomatal and xylem regulation. Nat. Geosci. 10, 284–288.
- 739 https://doi.org/10.1038/ngeo2903

- Körner, C., Morgan, J., Norby, R., 2007. CO2 Fertilization: When, Where, How Much?, in:
- 741 Canadell, J.G., Pataki, D.E., Pitelka, L.F. (Eds.), Terrestrial Ecosystems in a
- 742 Changing World, Global Change The IGBP Series. Springer, Berlin, Heidelberg,

743 pp. 9–21. https://doi.org/10.1007/978-3-540-32730-1_2

- Kramer, P.J., 1981. Carbon Dioxide Concentration, Photosynthesis, and Dry Matter
- 745 Production. BioScience 31, 29–33. https://doi.org/10.2307/1308175
- Kull, O., Kruijt, B., 1998. Leaf photosynthetic light response: a mechanistic model for scaling
- photosynthesis to leaves and canopies. Funct. Ecol. 12, 767–777.
- 748 https://doi.org/10.1046/j.1365-2435.1998.00257.x
- Kulmatiski, A., Adler, P.B., Foley, K.M., 2020. Hydrologic niches explain species coexistence
 and abundance in a shrub–steppe system. J. Ecol. 108, 998–1008.
- 751 https://doi.org/10.1111/1365-2745.13324
- Le Quéré, C., Andrew, R.M., Friedlingstein, P., Sitch, S., Pongratz, J., Manning, A.C.,
- 753 Korsbakken, J.I., Peters, G.P., Canadell, J.G., Jackson, R.B., Boden, T.A., Tans,
- 754 P.P., Andrews, O.D., Arora, V.K., Bakker, D.C.E., Barbero, L., Becker, M., Betts,
- 755 R.A., Bopp, L., Chevallier, F., Chini, L.P., Ciais, P., Cosca, C.E., Cross, J., Currie, K.,
- 756 Gasser, T., Harris, I., Hauck, J., Haverd, V., Houghton, R.A., Hunt, C.W., Hurtt, G.,
- 757 Ilyina, T., Jain, A.K., Kato, E., Kautz, M., Keeling, R.F., Klein Goldewijk, K.,
- 758 Körtzinger, A., Landschützer, P., Lefèvre, N., Lenton, A., Lienert, S., Lima, I.,
- Lombardozzi, D., Metzl, N., Millero, F., Monteiro, P.M.S., Munro, D.R., Nabel,
- 760 J.E.M.S., Nakaoka, S., Nojiri, Y., Padin, X.A., Peregon, A., Pfeil, B., Pierrot, D.,
- 761 Poulter, B., Rehder, G., Reimer, J., Rödenbeck, C., Schwinger, J., Séférian, R.,
- 762 Skjelvan, I., Stocker, B.D., Tian, H., Tilbrook, B., Tubiello, F.N., van der Laan-Luijkx,
- 763 I.T., van der Werf, G.R., van Heuven, S., Viovy, N., Vuichard, N., Walker, A.P.,
- 764 Watson, A.J., Wiltshire, A.J., Zaehle, S., Zhu, D., 2018. Global Carbon Budget 2017.
- 765 Earth Syst. Sci. Data 10, 405–448. https://doi.org/10.5194/essd-10-405-2018
- Leakey, A.D.B., Ainsworth, E.A., Bernacchi, C.J., Rogers, A., Long, S.P., Ort, D.R., 2009.
- 767 Elevated CO2 effects on plant carbon, nitrogen, and water relations: six important

- 768 lessons from FACE. J. Exp. Bot. 60, 2859–2876. https://doi.org/10.1093/jxb/erp096
- Lee, H., Park, J., Cho, S., Lee, M., Kim, H.S., 2019. Impact of leaf area index from various
- sources on estimating gross primary production in temperate forests using the
- JULES land surface model. Agric. For. Meteorol. 276–277, 107614.
- 772 https://doi.org/10.1016/j.agrformet.2019.107614
- T73 Lemordant, L., Gentine, P., Swann, A.S., Cook, B.I., Scheff, J., 2018. Critical impact of
- vegetation physiology on the continental hydrologic cycle in response to increasing
- 775 CO2. Proc. Natl. Acad. Sci. 115, 4093–4098.
- 776 https://doi.org/10.1073/pnas.1720712115
- Leuzinger, S., Körner, C., 2007. Water savings in mature deciduous forest trees under
 elevated CO2. Glob. Change Biol. 13, 2498–2508. https://doi.org/10.1111/j.13652486.2007.01467.x
- 2100.2001.01101.x
- Liu, J., You, Y., Li, J., Sitch, S., Gu, X., Nabel, J.E.M.S., Lombardozzi, D., Luo, M., Feng, X.,
- 781 Arneth, A., Jain, A.K., Friedlingstein, P., Tian, H., Poulter, B., Kong, D., 2021.
- 782 Response of global land evapotranspiration to climate change, elevated CO2, and
- 783 land use change. Agric. For. Meteorol. 311, 108663.
- 784 https://doi.org/10.1016/j.agrformet.2021.108663
- Long, S.P., 1991. Modification of the response of photosynthetic productivity to rising
- temperature by atmospheric CO2 concentrations: Has its importance been
- vunderestimated? Plant Cell Environ. 14, 729–739. https://doi.org/10.1111/j.1365-
- 788 3040.1991.tb01439.x
- Lundberg, S., Lee, S.-I., 2017. A Unified Approach to Interpreting Model Predictions.
- 790 ArXiv170507874 Cs Stat.
- Lundberg, S.M., Erion, G., Chen, H., DeGrave, A., Prutkin, J.M., Nair, B., Katz, R.,
- Himmelfarb, J., Bansal, N., Lee, S.-I., 2020. From local explanations to global
- understanding with explainable AI for trees. Nat. Mach. Intell. 2, 56–67.
- 794 https://doi.org/10.1038/s42256-019-0138-9
- 795 Maurer, G.E., Hallmark, A.J., Brown, R.F., Sala, O.E., Collins, S.L., 2020. Sensitivity of

primary production to precipitation across the United States. Ecol. Lett. 23, 527–536.

797 https://doi.org/10.1111/ele.13455

- McCarthy, H.R., Oren, R., Finzi, A.C., Johnsen, K.H., 2006. Canopy leaf area constrains
 [CO2]-induced enhancement of productivity and partitioning among aboveground
 carbon pools. Proc. Natl. Acad. Sci. 103, 19356–19361.
- 801 https://doi.org/10.1073/pnas.0609448103
- McCarthy, H.R., Oren, R., Johnsen, K.H., Gallet-Budynek, A., Pritchard, S.G., Cook, C.W.,
- LaDeau, S.L., Jackson, R.B., Finzi, A.C., 2010. Re-assessment of plant carbon
- 804 dynamics at the Duke free-air CO2 enrichment site: interactions of atmospheric
- 805 [CO2] with nitrogen and water availability over stand development. New Phytol. 185,
 806 514–528. https://doi.org/10.1111/j.1469-8137.2009.03078.x
- 807 Medlyn, B.E., Barton, C.V.M., Broadmeadow, M.S.J., Ceulemans, R., De Angelis, P.,
- 808 Forstreuter, M., Freeman, M., Jackson, S.B., Kellomäki, S., Laitat, E., Rey, A.,
- 809 Roberntz, P., Sigurdsson, B.D., Strassemeyer, J., Wang, K., Curtis, P.S., Jarvis,
- 810 P.G., 2001. Stomatal conductance of forest species after long-term exposure to
- elevated CO2 concentration: a synthesis. New Phytol. 149, 247–264.
- 812 https://doi.org/10.1046/j.1469-8137.2001.00028.x
- 813 Medlyn, B.E., Duursma, R.A., Eamus, D., Ellsworth, D.S., Prentice, I.C., Barton, C.V.M.,
- 814 Crous, K.Y., Angelis, P.D., Freeman, M., Wingate, L., 2011. Reconciling the optimal
- and empirical approaches to modelling stomatal conductance. Glob. Change Biol. 17,

816 2134–2144. https://doi.org/10.1111/j.1365-2486.2010.02375.x

- 817 Meehl, G.A., Moss, R., Taylor, K.E., Eyring, V., Stouffer, R.J., Bony, S., Stevens, B., 2014.
- 818 Climate Model Intercomparisons: Preparing for the Next Phase. Eos Trans. Am.
- 819 Geophys. Union 95, 77–78. https://doi.org/10.1002/2014EO090001
- 820 Migliavacca, M., Musavi, T., Mahecha, M.D., Nelson, J.A., Knauer, J., Baldocchi, D.D.,
- 821 Perez-Priego, O., Christiansen, R., Peters, J., Anderson, K., Bahn, M., Black, T.A.,
- Blanken, P.D., Bonal, D., Buchmann, N., Caldararu, S., Carrara, A., Carvalhais, N.,
- 823 Cescatti, A., Chen, J., Cleverly, J., Cremonese, E., Desai, A.R., El-Madany, T.S.,

824	Farella, M.M., Fernández-Martínez, M., Filippa, G., Forkel, M., Galvagno, M.,
825	Gomarasca, U., Gough, C.M., Göckede, M., Ibrom, A., Ikawa, H., Janssens, I.A.,
826	Jung, M., Kattge, J., Keenan, T.F., Knohl, A., Kobayashi, H., Kraemer, G., Law, B.E.,
827	Liddell, M.J., Ma, X., Mammarella, I., Martini, D., Macfarlane, C., Matteucci, G.,
828	Montagnani, L., Pabon-Moreno, D.E., Panigada, C., Papale, D., Pendall, E.,
829	Penuelas, J., Phillips, R.P., Reich, P.B., Rossini, M., Rotenberg, E., Scott, R.L.,
830	Stahl, C., Weber, U., Wohlfahrt, G., Wolf, S., Wright, I.J., Yakir, D., Zaehle, S.,
831	Reichstein, M., 2021. The three major axes of terrestrial ecosystem function. Nature
832	598, 468–472. https://doi.org/10.1038/s41586-021-03939-9
833	Miguez-Macho, G., Fan, Y., 2021. Spatiotemporal origin of soil water taken up by vegetation.
834	Nature 598, 624–628. https://doi.org/10.1038/s41586-021-03958-6
835	Norby, R.J., DeLucia, E.H., Gielen, B., Calfapietra, C., Giardina, C.P., King, J.S., Ledford, J.,
836	McCarthy, H.R., Moore, D.J.P., Ceulemans, R., Angelis, P.D., Finzi, A.C., Karnosky,
837	D.F., Kubiske, M.E., Lukac, M., Pregitzer, K.S., Scarascia-Mugnozza, G.E.,
838	Schlesinger, W.H., Oren, R., 2005. Forest response to elevated CO2 is conserved
839	across a broad range of productivity. Proc. Natl. Acad. Sci. 102, 18052–18056.
840	https://doi.org/10.1073/pnas.0509478102
841	Norby, R.J., Wullschleger, S.D., Gunderson, C.A., Johnson, D.W., Ceulemans, R., 1999.
842	Tree responses to rising CO2 in field experiments: implications for the future forest.
843	Plant Cell Environ. 22, 683–714. https://doi.org/10.1046/j.1365-3040.1999.00391.x
844	Norby, R.J., Zak, D.R., 2011. Ecological Lessons from Free-Air CO2 Enrichment (FACE)
845	Experiments. Annu. Rev. Ecol. Evol. Syst. 42, 181–203.
846	https://doi.org/10.1146/annurev-ecolsys-102209-144647
847	Novick, K.A., Ficklin, D.L., Stoy, P.C., Williams, C.A., Bohrer, G., Oishi, A.C., Papuga, S.A.,
848	Blanken, P.D., Noormets, A., Sulman, B.N., Scott, R.L., Wang, L., Phillips, R.P.,
849	2016. The increasing importance of atmospheric demand for ecosystem water and
850	carbon fluxes. Nat. Clim. Change 6, 1023–1027.
851	https://doi.org/10.1038/nclimate3114

- Pedregosa, F., Varoquaux, G., Gramfort, A., Michel, V., Thirion, B., Grisel, O., Blondel, M.,
- 853 Prettenhofer, P., Weiss, R., Dubourg, V., Vanderplas, J., Passos, A., Cournapeau,
- D., n.d. Scikit-learn: Machine Learning in Python. Mach. Learn. PYTHON 6.
- 855 Peñuelas, J., Canadell, J.G., Ogaya, R., 2011. Increased water-use efficiency during the
- 20th century did not translate into enhanced tree growth. Glob. Ecol. Biogeogr. 20,
- 857 597–608. https://doi.org/10.1111/j.1466-8238.2010.00608.x
- 858 Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M.D., Seneviratne, S.I.,
- Zscheischler, J., Beer, C., Buchmann, N., Frank, D.C., Papale, D., Rammig, A.,
- 860 Smith, P., Thonicke, K., van der Velde, M., Vicca, S., Walz, A., Wattenbach, M.,
- 2013. Climate extremes and the carbon cycle. Nature 500, 287–295.
- 862 https://doi.org/10.1038/nature12350
- 863 Saxton, K.E., Rawls, W.J., 2006. Soil Water Characteristic Estimates by Texture and
- 864 Organic Matter for Hydrologic Solutions. Soil Sci. Soc. Am. J. 70, 1569–1578.
 865 https://doi.org/10.2136/sssaj2005.0117
- Schimel, D., Stephens, B.B., Fisher, J.B., 2015. Effect of increasing CO2 on the terrestrial
 carbon cycle. Proc. Natl. Acad. Sci. 112, 436–441.
- 868 https://doi.org/10.1073/pnas.1407302112
- Street, L.E., Shaver, G.R., Williams, M., Van Wijk, M.T., 2007. What is the relationship
- between changes in canopy leaf area and changes in photosynthetic CO2 flux in
- 871 arctic ecosystems? J. Ecol. 95, 139–150. https://doi.org/10.1111/j.1365-
- 872 2745.2006.01187.x
- Thum, T., Caldararu, S., Engel, J., Kern, M., Pallandt, M., Schnur, R., Yu, L., Zaehle, S.,
- 874 2019. A new model of the coupled carbon, nitrogen, and phosphorus cycles in the
- 875 terrestrial biosphere (QUINCY v1.0; revision 1996). Geosci. Model Dev. 12, 4781–
- 876 4802. https://doi.org/10.5194/gmd-12-4781-2019
- 877 Ueyama, M., Ichii, K., Kobayashi, H., Kumagai, T., Beringer, J., Merbold, L., Euskirchen,
- 878 E.S., Hirano, T., Marchesini, L.B., Baldocchi, D., Saitoh, T.M., Mizoguchi, Y., Ono, K.,
- Kim, J., Varlagin, A., Kang, M., Shimizu, T., Kosugi, Y., Bret-Harte, M.S., Machimura,

880	T., Matsuura, Y., Ohta, T., Takagi, K., Takanashi, S., Yasuda, Y., 2020. Inferring
881	CO2 fertilization effect based on global monitoring land-atmosphere exchange with a
882	theoretical model. Environ. Res. Lett. 15, 084009. https://doi.org/10.1088/1748-
883	9326/ab79e5
884	van der Sleen, P., Groenendijk, P., Vlam, M., Anten, N.P.R., Boom, A., Bongers, F., Pons,
885	T.L., Terburg, G., Zuidema, P.A., 2015. No growth stimulation of tropical trees by 150
886	years of CO2 fertilization but water-use efficiency increased. Nat. Geosci. 8, 24–28.
887	https://doi.org/10.1038/ngeo2313
888	Walker, A.P., De Kauwe, M.G., Medlyn, B.E., Zaehle, S., Iversen, C.M., Asao, S., Guenet,
889	B., Harper, A., Hickler, T., Hungate, B.A., Jain, A.K., Luo, Y., Lu, X., Lu, M., Luus, K.,
890	Megonigal, J.P., Oren, R., Ryan, E., Shu, S., Talhelm, A., Wang, YP., Warren, J.M.,
891	Werner, C., Xia, J., Yang, B., Zak, D.R., Norby, R.J., 2019. Decadal biomass
892	increment in early secondary succession woody ecosystems is increased by CO2
893	enrichment. Nat. Commun. 10, 454. https://doi.org/10.1038/s41467-019-08348-1
894	Walker, A.P., Kauwe, M.G.D., Bastos, A., Belmecheri, S., Georgiou, K., Keeling, R.F.,
895	McMahon, S.M., Medlyn, B.E., Moore, D.J.P., Norby, R.J., Zaehle, S., Anderson-
896	Teixeira, K.J., Battipaglia, G., Brienen, R.J.W., Cabugao, K.G., Cailleret, M.,
897	Campbell, E., Canadell, J.G., Ciais, P., Craig, M.E., Ellsworth, D.S., Farquhar, G.D.,
898	Fatichi, S., Fisher, J.B., Frank, D.C., Graven, H., Gu, L., Haverd, V., Heilman, K.,
899	Heimann, M., Hungate, B.A., Iversen, C.M., Joos, F., Jiang, M., Keenan, T.F.,
900	Knauer, J., Körner, C., Leshyk, V.O., Leuzinger, S., Liu, Y., MacBean, N., Malhi, Y.,
901	McVicar, T.R., Penuelas, J., Pongratz, J., Powell, A.S., Riutta, T., Sabot, M.E.B.,
902	Schleucher, J., Sitch, S., Smith, W.K., Sulman, B., Taylor, B., Terrer, C., Torn, M.S.,
903	Treseder, K.K., Trugman, A.T., Trumbore, S.E., Mantgem, P.J. van, Voelker, S.L.,
904	Whelan, M.E., Zuidema, P.A., 2021. Integrating the evidence for a terrestrial carbon
905	sink caused by increasing atmospheric CO2. New Phytol. 229, 2413–2445.
906	https://doi.org/10.1111/nph.16866

907 Way, D.A., Katul, G.G., Manzoni, S., Vico, G., 2014. Increasing water use efficiency along

- 908 the C3 to C4 evolutionary pathway: a stomatal optimization perspective. J. Exp. Bot.
- 909 65, 3683–3693. https://doi.org/10.1093/jxb/eru205
- 910 Weisstein, Eric W. (n.d.)."Least Squares Fitting." From MathWorld--A Wolfram Web

911 Resource. https://mathworld.wolfram.com/LeastSquaresFitting.html

- 912 Williams, I.N., Torn, M.S., 2015. Vegetation controls on surface heat flux partitioning, and
- 913 land-atmosphere coupling. Geophys. Res. Lett. 42, 9416–9424.
- 914 https://doi.org/10.1002/2015GL066305
- 915 Winkler, A.J., Myneni, R.B., Hannart, A., Sitch, S., Haverd, V., Lombardozzi, D., Arora, V.K.,
- 916 Pongratz, J., Nabel, J.E.M.S., Goll, D.S., Kato, E., Tian, H., Arneth, A., Friedlingstein,
- 917 P., Jain, A.K., Zaehle, S., Brovkin, V., 2021. Slowdown of the greening trend in
- 918 natural vegetation with further rise in atmospheric CO₂. Biogeosciences 18, 4985–
- 919 5010. https://doi.org/10.5194/bg-18-4985-2021
- Woodward, F.I., Kelly, C.K., 1995. The influence of CO2 concentration on stomatal density.
 New Phytol. 131, 311–327. https://doi.org/10.1111/j.1469-8137.1995.tb03067.x
- 922 Wullschleger, S.D., Tschaplinski, T.J., Norby, R.J., 2002. Plant water relations at elevated
- 923 CO2– implications for water-limited environments. Plant Cell Environ. 25, 319–331.
- 924 https://doi.org/10.1046/j.1365-3040.2002.00796.x
- 925 Zaehle, S., Friend, A.D., 2010. Carbon and nitrogen cycle dynamics in the O-CN land
- 926 surface model: 1. Model description, site-scale evaluation, and sensitivity to
- 927 parameter estimates. Glob. Biogeochem. Cycles 24.
- 928 https://doi.org/10.1029/2009GB003521

1 Supplemental materials

2 Table S1 Vegetation classes used in this study.

Vegetation classes	Plant functional types (PFTs) defined in the QUINCY model
Tropical Forest	Tropical broadleaf evergreen (TrBE)
	Tropical broadleaf rain deciduous (TrBR)
Temperate Forest	Temperate broadleaf evergreen (TeBE)
	Temperate broadleaf summer green (TeBS)
Boreal Forest	Boreal needleleaf evergreen (BNE)
	Boreal needleleaf summer green (BNS)
Grass	C3 grass (TeH)
	C4 grass (TrH)



Fig. S1 Differences in annual average light-use efficiency (LUE) between the transient-CO₂ and the constant-CO₂ experiments across climate and vegetation classes. Analogous to Fig. 2 but with additional grouping of sites by precipitation using quantiles (low in dotted line: ≤ 0.33 ; middle in dashed line: 0.33 - 0.66; high in solid line: ≥ 0.66).





Fig. S2 Differences in annual average GPP between the transient-CO₂ and the
 constant-CO₂ experiments across climate and vegetation classes. Analogous
 to Fig. S1.



15 Fig. S3 Differences in annual average Tr_{norm} between the transient-CO₂ and the

16 constant-CO₂ experiments across climate and vegetation classes. Analogous to

17 Fig. S1.



18

- 19 Fig. S4 Spatial distribution of EoC in GPP while changing the number (n = 3, 5,
- 20 **7, 9) of consecutive years in the definition of EoC (section 2.2.2).**



Fig. S5 Global distribution of EoC in light-use efficiency (LUE). Bright color indicates an earlier detection (lower EoC), and dark color indicates a later detection

(higher EoC). Non-colored points indicate sites where the elevated CO₂ does not
 translate into significant GPP changes within the historical time period.

26



27

Fig. S6 Global distribution of EoC in GPP in recent years. Analogous to Fig. 4 but the EoC is derived from the transient-CO₂ and freeze-CO₂ experiments (see section

30 2.1.2.2).



Fig. S7 Temporal variation in EoC in GPP across the seasonal and daily cycle. Insets show so-called fingerprint plots illustrating EoC along the seasonal (*y*-axis) and diurnal cycle (*x*-axis) at representative sites for the vegetation classes (a) Boreal Forest, (b) Tropical Forest, (c) Grass and (d) Temperate Forest. The gray points on the map refer to the geographical locations of the four sites.



37

Fig. S8 Global distribution of EoC in LAI (a), biomass (b), NPP (c) and evaporation (d). Bright color indicates an earlier detection (lower EoC), and dark color indicates a later detection (higher EoC). Non-colored points indicate sites where the elevated CO₂ does not translate into significant GPP changes within the historical time period.



Fig. S9 Analogous to Fig. 5 but for different vegetation types. The dashed yellow
line connects each point showing the mean EoC in each variable and metric. The
definition of vegetation groups is the same as in Fig. 2.



48 Fig. S10 Variable importance explaining the spatial patterns of EoC in GPP and

49 Trnorm. The figure shows the mean SHAP values from 1000 simulations based on a

random forest model to examine the variables that explain the spatial variability of EoC in (a) GPP and (b) Tr_{norm}. The variables used as predictors are the long-term mean values of each variable. The average Out of Bag (oob) score indicates the random forest model performance and can be interpreted as the explained fraction of the variance of the target variable.



55

56 Fig. S11 EoC in GPP across the participating CMIP6 models and QUINCY. EoC

in GPP is plotted against the long-term mean LAI, and each dot represents the grid cell value in closest proximity to the particular QUINCY site. The red line refers to the

59 least-squares regression best-fit.





Fig. S12 EoC in Trnorm across the participating CMIP6 models and QUINCY. EoC

62 in Tr_{norm} is plotted against the long-term mean GPP, and each dot represents the grid-

63 cell value in closest proximity to the particular QUINCY site. The red line refers to the

64 least-squares regression best-fit.