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Robust response of terrestrial plants to rising CO2
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Abstract:	Human-caused CO2 emissions over the last century have caused Earth's climate to warm, and directly impacted the functioning of terrestrial plants. We examine the global response of terrestrial gross primary productivity (GPP) to the historic change in atmospheric CO2. The GPP of the terrestrial biosphere has increased steadily, keeping pace remarkably in proportion to the rise in atmospheric CO2. Water-use efficiency, the ratio of CO2 uptake by photosynthesis to water loss by transpiration, has increased as a direct leaf-level effect of rising CO2. This has allowed an increase in global leaf area, which has conspired with stimulation of photosynthesis per unit leaf area to produce a maximal response of the terrestrial biosphere to rising atmospheric CO2 and contemporary climate change.

Robust response of terrestrial plants to rising CO_2

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Abstract

Human-caused CO_2 emissions over the last century have caused Earth's climate to warm, and directly impacted the functioning of terrestrial plants. We examine the global response of terrestrial gross primary production (GPP) to the historic change in atmospheric CO_2. The GPP of the terrestrial biosphere has increased steadily, keeping pace remarkably in proportion to the rise in atmospheric CO_2. Water-use efficiency, the ratio of CO_2 uptake by photosynthesis to water loss by transpiration, has increased as a direct leaf-level effect of rising CO_2. This has allowed an increase in global leaf area, which has conspired with stimulation of photosynthesis per unit leaf area to produce a maximal response of the terrestrial biosphere to rising atmospheric CO_2 and contemporary climate change.

Highlights

Global climate change caused by CO_2 emissions can stress terrestrial vegetation, potentially decreasing production. On the other hand, CO_2 interacts directly with plants, stimulating leaf-level photosynthesis and water-use efficiency.

The rise in atmospheric CO_2 concentration over the last century presents an opportunity for gauging the strength of the terrestrial biosphere response in light of these potential impacts.

An atmospheric proxy and model analysis both suggest that global terrestrial photosynthesis has increased in nearly constant proportion to the rise in atmospheric CO_2 concentration, a maximal response by the terrestrial biosphere.

An accurate understanding of the impacts of climate change on terrestrial vegetation is essential for managing risks associated with human-caused climate change; gauging the historic response of terrestrial photosynthesis is an important step in this direction.

Key words: carbon dioxide, global climate change, greenhouse effect, photosynthesis

Rising atmospheric CO_2 and global climate change

Emissions of CO_2 associated with human industrial activity and land-use change over the last century have significantly impacted global climate, causing global warming of about 1.0°C [1]. The anthropogenic CO_2 emission rate is continuing to increase and the future rise in atmospheric CO_2 will undoubtedly lead to more climate change, including increases in the frequency of extreme climate events such as heat waves, droughts, and storms [2]. Global climate change has the potential to significantly stress terrestrial vegetation [3], for example with hot, dry air, soil moisture deficits, or flooding. This could lead to a carbon-climate feedback in which widespread tree mortality and forest decline contribute to an accelerating accumulation of CO_2 in the atmosphere [4-6].

On the other hand, plants interact directly with atmospheric CO_2, and they can potentially respond to rising atmospheric CO_2 concentrations by increasing photosynthetic rates and water-use efficiency [7-10]. Water-use efficiency in this context is defined as the amount of CO_2 taken up by photosynthesis for a given amount of water lost to the atmosphere by transpiration (Box 1). Understanding emergent responses of the production of terrestrial vegetation to the potentially opposing impacts of global climate change and CO_2 fertilization is critical for formulating effective mitigation and adaptation strategies [11].

On the global scale, there is currently an imbalance between the amount of CO_2 absorbed by the terrestrial biosphere through photosynthesis and the amount released back to the atmosphere through plant respiration, decomposition, fire, and emissions from land-use change [12]. This is commonly referred to as the land carbon sink. It is slowing the rate of increase in atmospheric CO_2 that would otherwise result from anthropogenic CO_2 emissions. Predicting the future behavior of the land carbon sink is one of the most important challenges in carbon cycle science, due to the potential for feedbacks that could accelerate the rate of future climate change [13]. This requires a robust understanding of the process through which the terrestrial biosphere captures CO_2: photosynthesis.

The response of terrestrial GPP over the last century

Gross primary production (GPP) is the total amount of CO_2 absorbed by photosynthesis per unit time. Examining the GPP response to historic changes in atmospheric CO_2 can provide useful insight into how the terrestrial biosphere has responded to human-caused CO_2 emissions and global climate change so far. The concentration of atmospheric CO_2 has risen from 280 ppm at the start of the industrial revolution to about 410 ppm today. Most of this increase has taken place since the start of the twentieth century. This greater than 40% increase in atmospheric CO_2 concentration provides a global scale experiment that has allowed scientists to assess the response of GPP to higher CO_2 levels.

Recently, a sulfur-containing analog of CO_2 in the atmosphere called carbonyl sulfide was used to estimate the historical, proportional increase in global GPP over the last century [14]. Carbonyl sulfide in the atmosphere, with oceanic and anthropogenic sources, shows seasonal and diurnal cycles and a long-term trend which can be related to its flux into leaves when they are photosynthetically active [15-17]. Thus, it behaves similarly to CO_2 with respect to uptake by photosynthesis, but is destroyed once it has entered the leaf, and therefore does not have a return flux from leaf to atmosphere that would be analogous to respiration. For this reason, it works well as a tracer for GPP insofar as it is free of the

80 complication of having simultaneous fluxes into and out of plants at the same time as occurs
81 with CO_2. The proportional increase in GPP from the year 1900 to 2013 based on the
82 carbonyl sulfide atmospheric budget was estimated to be $31 \pm 5\%$ [14], which is directly
83 proportional to the increase in atmospheric CO_2 concentration (Figure 1).

84   This suggests that the photosynthetic activity of the terrestrial biosphere has kept pace
85 remarkably with the historic rise in atmospheric CO_2 concentration and its associated climate
86 change. In order to better understand this intriguing result, we applied the Community
87 Atmosphere–Biosphere Land Exchange model (CABLE) to the historic time period of
88 interest [18]. This model was recently shown to outperform a range of terrestrial biosphere
89 models in its ability to correctly simulate the twentieth century increase in global GPP as
90 deduced from the carbonyl sulfide atmospheric constraint (Haverd et al, in review). The
91 analysis by CABLE suggests that the largest proportion of GPP growth resulted from a direct
92 effect of CO_2 fertilization on photosynthesis rates (Figure 2a), and that there were additional
93 effects associated with greening, an increase in leaf area, which took place mainly in semi-
94 arid regions, and with climate change. In gauging strength of this response of GPP in the
95 terrestrial biosphere to rising CO_2 and climate change, we find that a very simplified
96 mathematical description, as shown in Box 1, can help to put it into context.

97

98 **Box 1**

99   Plant physiological theory predicts that photosynthesis and water-use efficiency
100 should increase as the CO_2 concentration surrounding a leaf increases [7, 19, 20]. Although
101 simple in formulation, this theory can explain some of the most impactful changes in the
102 functioning of terrestrial plants in response to rising atmospheric CO_2. Fick's law of
103 diffusion provides one basis for a mathematical description of photosynthesis:

104
$$A = g_c(c_a - c_i) \, , \qquad (1)$$

105 where A is the net rate of CO_2 assimilation by photosynthesis, g_c is the stomatal conductance
106 to CO_2, c_a is the CO_2 concentration in the air outside the leaf, and c_i is the CO_2 concentration
107 in the leaf intercellular air spaces. This equation can also be written as,

108
$$A = c_a g_c \left(1 - \frac{c_i}{c_a}\right). \qquad (2)$$

109 Equation 2 is useful because it shows that if g_c and c_i/c_a remain approximately constant, then
110 A will increase in direct proportion to an increase in c_a. We consider such a constant
111 proportional response to be a maximal response of A to changing c_a. It implies no
112 downregulation of photosynthetic capacity in response to the increase in c_a, and no stomatal
113 closure in response to the increase in c_a that would otherwise restrict the diffusion of CO_2 into
114 the leaf and slow the increase of photosynthesis. A similar diffusion equation can be written
115 for the transpiration rate (E):

116
$$E = g_s(w_i - w_a) \, , \qquad (3)$$

117 where g_s is stomatal conductance to water vapour, which is typically taken as $1.6g_c$ due to
118 H_2O molecules diffusing faster compared to CO_2. The w_i is the water vapour concentration

119 in the intercellular air spaces inside the leaf, and w_a is that in the air outside the leaf.
120 Dividing equation 2 by equation 3 yields an expression for water-use efficiency (A/E):

$$\frac{A}{E} = \frac{c_a\left(1-\frac{c_i}{c_a}\right)}{1.6(w_i-w_a)}. \tag{4}$$

122 Equation 4 shows that there are two processes which modify the response of A/E to c_a, these
123 being c_i/c_a and the leaf-to-air water vapour concentration difference, w_i-w_a.

124   Time-integrated estimates of c_i/c_a can be obtained by measuring carbon isotope
125 discrimination ($\Delta^{13}C$) with respect to atmospheric CO_2 in C_3 plants [21-23]. The equation
126 relating the two is:

$$\Delta^{13}C = a + (b - a)\frac{c_i}{c_a}, \tag{5}$$

128 where a is the $^{13}C/^{12}C$ fractionation that occurs during diffusion of CO_2 through stomata
129 (4.4‰) and b is the fractionation that occurs during carboxylation by Rubisco (27‰). The
130 $\Delta^{13}C$ can be measured in plant dry mass and provides an integrated record of c_i/c_a over the
131 period during which the tissue was formed [24].

132

Contextualizing the GPP response

134   Taking a reductionist approach, the response of the terrestrial biosphere to twentieth
135 century climate change can be abstracted to that of a single leaf. By replacing A in equation 2
136 with GPP, one then obtains the surprising result that the globally scaled term $g_c(1-c_i/c_a)$
137 would need to have remained approximately constant to explain the observed increase in GPP
138 over the last century, because GPP has increased in nearly constant proportion to the increase
139 in c_a (Figure 1 and Box 1). Such an abstraction ignores several processes known to be
140 important to photosynthesis, *e.g.* mesophyll conductance [25], but we note that the overall
141 thrust of our argument would not change if these processes were also taken into account.

142   The c_i/c_a is the ratio of intercellular to ambient CO_2 concentrations during
143 photosynthesis. Because photosynthetic enzymes consume CO_2 inside the leaf, the
144 concentration of CO_2 in the air spaces inside leaves, c_i, decreases below the ambient
145 concentration, c_a. The proportional reduction in c_i relative to c_a can be considered a gas
146 exchange set point, a diagnostic feature of the photosynthetic behavior of terrestrial plants
147 [26]. Assessing variation in this attribute has been greatly facilitated by the relationship
148 between carbon isotope discrimination ($\Delta^{13}C$) and c_i/c_a in plants which use the C_3
149 photosynthetic pathway (Box 1). Plants using the C_3 photosynthetic pathway make up most
150 of the biomass in the terrestrial biosphere [27].

151   Multiple lines of evidence support the idea that c_i/c_a has remained approximately
152 constant as c_a increased over the last century. The $\Delta^{13}C$ measured in tree rings of both
153 temperate and tropical trees predominantly supports this contention [28-33], although
154 exceptions can also be found [34, 35]. Figure 3a shows the pattern of c_i/c_a inferred for trees
155 growing at three tropical forest sites, consistent with the notion of little to no change in c_i/c_a
156 over several decades of rising c_a. In this study the authors employed a sampling strategy such
157 that trees of similar age were compared across different decades. This is important because
158 $\Delta^{13}C$ can also show directional changes in response to increasing tree height [36, 37]; thus,

159 the height effect should ideally be removed from analyses aiming to test the singular response
160 of c_i/c_a to changes in c_a.

161   Although less common, analyses of $\Delta^{13}C$ in herbarium leaves can also be used to test
162 whether c_i/c_a has changed over the last century. As with tree ring results, these studies are
163 consistent with the idea of a relatively constant c_i/c_a in response to rising atmospheric CO_2
164 concentration over the twentieth century [38-40].

165   A recent analysis of the $^{13}C/^{12}C$ ratio in atmospheric CO_2 over the last century also
166 corroborated the trend of an approximately constant c_i/c_a in leaves of terrestrial plants as the
167 atmospheric CO_2 concentration increased [41]. This led the authors to conclude that globally,
168 A/g_c of land plants [equivalent to $c_a(1-c_i/c_a)$] has increased in nearly constant proportion to
169 the increase in c_a.

170   Assuming, as the above evidence suggests, that c_i/c_a has changed little in land plants
171 in response to rising c_a, Equation 2 indicates that the global, big-leaf analogy for stomatal
172 conductance must also have changed little. This is surprising because stomatal conductance
173 is known to decrease in response to increasing c_a [10, 20, 42-44]. The response can involve
174 both morphological and physiological components [19]. For example, maximum stomatal
175 conductance was shown to decrease across a range of species due to decreases in both
176 stomatal density and stomatal pore size [45-49], as shown in Figure 3b for a range of
177 subtropical tree species over the last century [45]. In addition, stomatal conductance is
178 known to decrease in response to CO_2 in short term exposure experiments [50].

179   If A is replaced with global annual GPP in Equation 2 then g_c becomes the global
180 conductance to CO_2 per unit ground area summed annually rather than being an instantaneous
181 conductance per unit leaf area. Then the result of constant global annual conductance
182 suggests that the total leaf area of terrestrial plants and the average length of the growing
183 season have increased in such a way so as to offset the likely reduction in stomatal
184 conductance per unit leaf area and time caused by increasing c_a (Figure 3b). This is
185 consistent with remotely sensed observations of greening of the global land surface [51-53],
186 observed increases in growing-season length especially in the northern hemisphere [54, 55],
187 and with the CABLE simulations (Figure 2a). These observations and modeling analyses
188 suggest that CO_2 fertilization has driven increases in leaf area index in the tropics, whereas
189 global warming has driven increases in leaf area index and growing-season length in high
190 latitude ecosystems.

191

Water-use efficiency has risen markedly

193   The term A/g_s is often referred to as intrinsic water-use efficiency, because it does not
194 depend on the leaf-to-air water vapour concentration difference, w_i-w_a. As can be seen from
195 Equation 2, if c_i/c_a remains constant in response to increasing c_a, then A/g_s will increase in
196 constant proportion to the increase in c_a. However, an important question arises as to how the
197 realized water-use efficiency A/E has responded, because w_i-w_a could also have increased
198 with global warming. As seen in Equation 4, an increase in w_i-w_a will cause a reduction in
199 A/E. The w_i-w_a might have increased for two reasons. First, air vapour pressure deficit is
200 likely to increase with global warming due to the potential for warmer air to hold more water
201 vapour. Second, the difference between leaf temperature and air temperature is also likely to

202 increase if stomata close somewhat in response to rising c_a, due to less evaporative cooling of
203 the leaf by transpiration. Thus, the response of A/E to rising c_a depends on competing effects
204 of increasing A/g_s and increasing $w_i - w_a$.

205   We used the CABLE model to gain insight into this question. The simulation
206 suggested that the increase in global transpiration with the twentieth century rise in c_a and
207 associated global warming was relatively modest (Figure 2b). Thus GPP/E, the ratio of
208 global gross primary production to global transpiration, showed a marked increase according
209 to the model simulation (Figure 2c). This is consistent with other recent model analyses
210 which showed similarly modest impacts of CO_2-induced global warming on transpiration,
211 and therefore strong impacts on A/E or its global analog GPP/E [9, 42, 56].
212 Evapotranspiration, the sum of transpiration and soil evaporation, decreased by about 2%
213 over the simulated time period, such that if water-use efficiency were expressed as GPP
214 divided by evapotranspiration, the increasing trend with time would have been even slightly
215 stronger than that for GPP/E.

216   Direct measurements of ecosystem-level CO_2 and water vapour fluxes through eddy
217 covariance also show strong increases in ecosystem water-use efficiency over the last three
218 decades [9, 57-60]. And consistent with results in Figure 2, a recent global analysis, which
219 combined ground-based and remotely sensed land and atmospheric observations, showed that
220 increasing water-use efficiency stimulated GPP directly, and also led to increasing leaf area
221 index, accounting for further gains in GPP [58].

222

Concluding remarks and future perspectives

224   Recent analyses suggest that the terrestrial biosphere has responded to anthropogenic
225 CO_2 emissions over the last century with a maximal increase in photosynthetic activity that
226 proportionally matched the increase in atmospheric CO_2 concentration. This partly resulted
227 from a marked increase in leaf-level photosynthesis and water-use efficiency, which
228 stimulated increases in leaf area in water-limited environments, while rising temperatures
229 lengthened growing seasons at high latitudes. The increases in global leaf area and in
230 growing season length approximately offset the impact of decreasing stomatal conductance at
231 the leaf level, such that the global conductance per unit ground area summed annually
232 remained nearly constant.

233   Increasing plant water-use efficiency is likely to strongly impact the future
234 functioning of terrestrial ecosystems under rising c_a, with potential to mitigate impact of
235 drought stress on vegetation caused by global warming [8, 61]. In addition, the strength of
236 the global land carbon sink has been shown to be sensitive to water storage on land, with
237 drier years being associated with a smaller sink [62]. Thus, future increases in plant water-
238 use efficiency will likely play a role modulating the land carbon sink.

239   An important outstanding question that emerges from our analysis is whether the
240 observed trend of GPP increasing in nearly constant proportion to c_a will continue with future
241 increases in c_a. The present day value of c_a is about 410 ppm, and this could double by the
242 end of the twenty-first century. Over this range, it seems likely that GPP growth will slow
243 due to saturating photosynthesis, nutrient limitations, or leaf area reaching a maximum per
244 unit ground area. Knowing when the slowing will start and to what extent it will depress

245 GPP growth will be critical for evaluations of carbon cycle feedbacks to future global
246 warming.

247   A second important question is the extent to which increases in GPP will stimulate net
248 primary production (NPP), the response that can most effectively produce a terrestrial carbon
249 sink. Some CO_2 enrichment experiments have indicated that nutrient and water availability
250 limit the NPP response to elevated CO_2 more so than the GPP response [63-67]. Here, the
251 extra carbon captured by photosynthesis rapidly cycled back to the atmosphere, through
252 microbial respiration of root exudates or ephemeral plant parts, such as leaves, fine roots, and
253 mycorrhizae [68-70]. Given these experimental results, it could be expected that the land
254 carbon sink will not increase proportionally with GPP growth in response to rising c_a.

255   Global climate change caused by CO_2 emissions carries tremendous risks for human
256 society. In this opinion article, we argue that terrestrial plants have responded vigorously to
257 the historic increase in atmospheric CO_2, and that adverse impacts of global climate change
258 on terrestrial plant production have been surpassed by the positive effects of CO_2 fertilization
259 at the global scale. However, this should not be interpreted as lessening the urgency with
260 which global climate change should be addressed by drastically and rapidly reducing human-
261 caused CO_2 emissions [2].

262

263 **Outstanding questions**

264   Can terrestrial plants continue to coordinate investment of nutrient resources into
265 different components of the photosynthetic process such that CO_2 assimilation rates continue
266 to increase as ambient CO_2 concentration continues rising?

267   Will availability of mineral nutrients become progressively limiting to photosynthesis
268 as atmospheric CO_2 concentrations become less limiting?

269   Will leaf area index (leaf area per unit ground area) saturate in the future, especially in
270 tropical biomes?

271   How is land use change impacting the trajectory of the photosynthetic response of the
272 terrestrial biosphere to rising CO_2 and climate change?

273   Will the response of NPP to rising CO_2 slow before that of GPP, diminishing the
274 growth of the land carbon sink more quickly than the growth of terrestrial photosynthesis?

275

283

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456

457   **Figure legends**

458   **Figure 1.** The proportional changes in gross primary production (GPP) from 1900 to 2013
459   inferred from carbonyl sulfide (COS) in the atmosphere (red dot), and predicted by a global
460   land-surface model, CABLE [18] (black line). The error bars on the red dot represent the
461   95% confidence interval around the COS-based estimate of the proportional change in GPP
462   [14]. The gold line shows the proportional increase in atmospheric CO_2 concentration over
463   the same time period.

464   **Figure 2.** (a) Attribution of changes in gross primary production (GPP) of the terrestrial
465   biosphere to leaf-level stimulation of photosynthesis, increasing leaf area (greening), and
466   changing climate, as simulated by the land-surface model CABLE [18]. (b) Changes in
467   global transpiration (E) with the same attributions as in panel a. (c) Changes in global water-
468   use efficiency, calculated as global GPP divided by global transpiration, with attributions as
469   described for panel a.

470   **Figure 3.** Examples of trends in c_i/c_a inferred from carbon isotope ratios of tree rings (a) and
471   maximum g_s calculated from leaf anatomical dimensions of stomatal density and stomatal
472   pore size (b). Data in panel a are from van der Sleen et al. [29] and those in panel b are from
473   Lammertsma et al. [45]. The blue lines in each panel show individual species responses and
474   the red lines show mean responses of all species.

475   **Box 1 Figure.** Three possible scenarios that could occur for the photosynthesis rate (a) and
476   the water-use efficiency (b) of a leaf in response to rising atmospheric CO_2 concentration (c_a).
477   In panel a, the maximal response occurs when both c_i/c_a and stomatal conductance do not
478   change in response to rising c_a. In panel b, the maximal response occurs when c_i/c_a and
479    $w_i - w_a$ do not change in response to rising c_a.

480

481   **Glossary**

482   **Carbon isotope discrimination ($\Delta^{13}C$):** the extent to which the $^{13}C/^{12}C$ ratio of
483   photosynthetically assimilated carbon differs from that of the atmospheric CO_2 which
484   provided the substrate for photosynthesis.

485   **Carbonyl sulfide (COS):** a trace gas in the atmosphere which is destroyed by enzymes
486   inside leaves that are active during photosynthesis. For this reason COS consumption by
487   leaves can be linked to CO_2 assimilation by photosynthesis.

488   **Gross primary production (GPP):** the total amount of carbon captured by photosynthesis
489   per unit area and time. By subtracting plant respiration from GPP, one obtains net primary
490   production (NPP), the total amount of carbon in new plant biomass per unit area and time.

491   **Intercellular to ambient CO_2 fraction (c_i/c_a):** the ratio of the CO_2 concentration in the
492   intercellular air spaces inside a leaf to that in the atmosphere outside the leaf. It is a measure
493   of the balance between the supply of CO_2 by stomata and its consumption by photosynthesis.

494   **Land carbon sink:** difference between the amount of carbon taken up by terrestrial
495   photosynthesis and that returned to the atmosphere through natural emission processes and
496   land use change.

497   **Leaf area index (LAI):** the one-sided, or projected, area of green leaves per unit ground
498   surface area.

499   **Leaf-to-air water vapour concentration difference (w_i-w_a):** the difference between the
500   water vapour mole fraction in the intercellular air spaces inside a leaf and that in the
501   atmosphere outside the leaf. It is the driving gradient for transpiration.

502   **Stomatal conductance (g_s, g_c):** the rate of CO_2 diffusion into or water vapour diffusion out
503   of a leaf relative to the concentration gradient driving diffusion. It is controlled by the
504   number, size and openness of stomatal pores. The stomatal conductance to water vapour (g_s)
505   is 1.6 times that for CO_2 (g_c), due to the different sizes of the molecules.

506   **Water-use efficiency:** the amount of carbon taken up by plants through photosynthesis for a
507   given amount of water vapour lost to the atmosphere by transpiration.
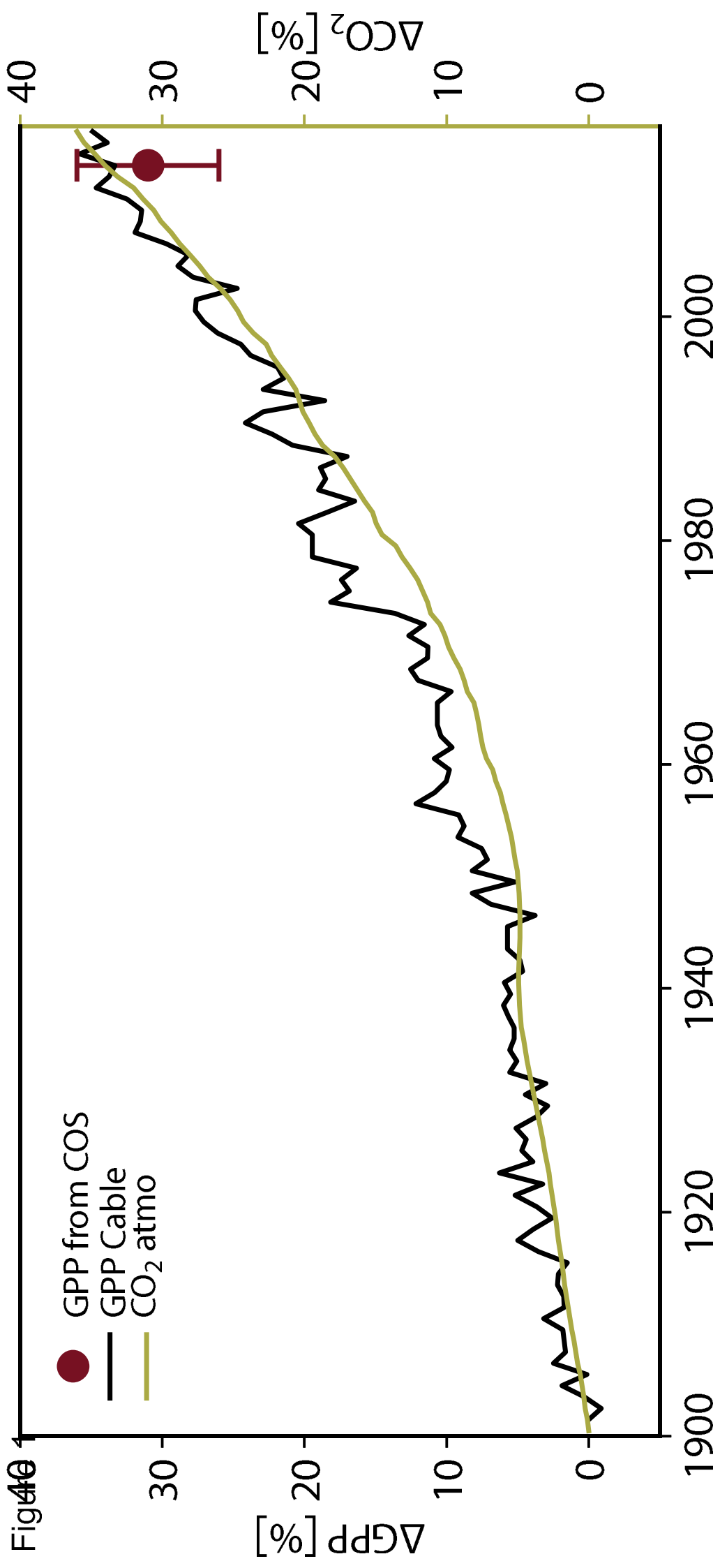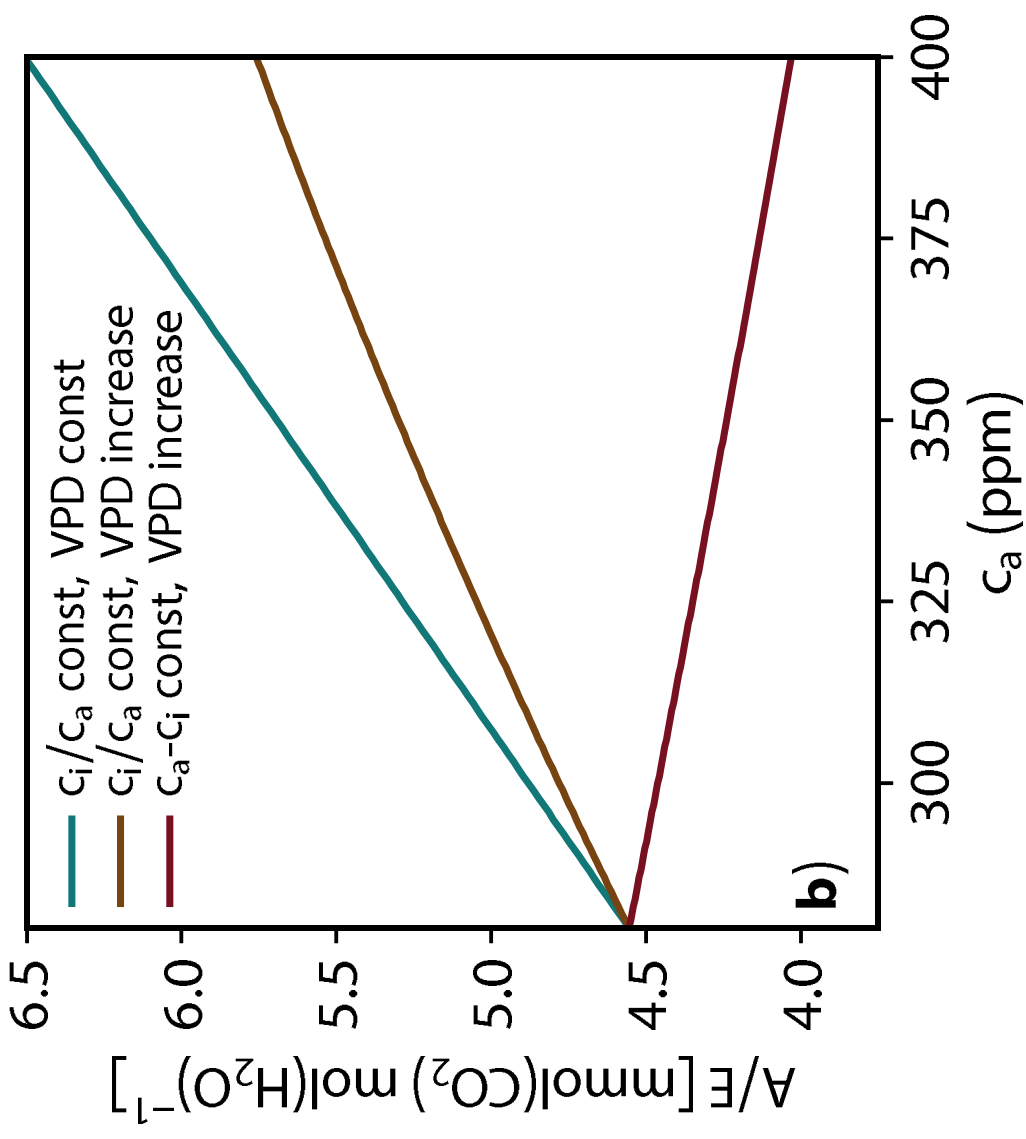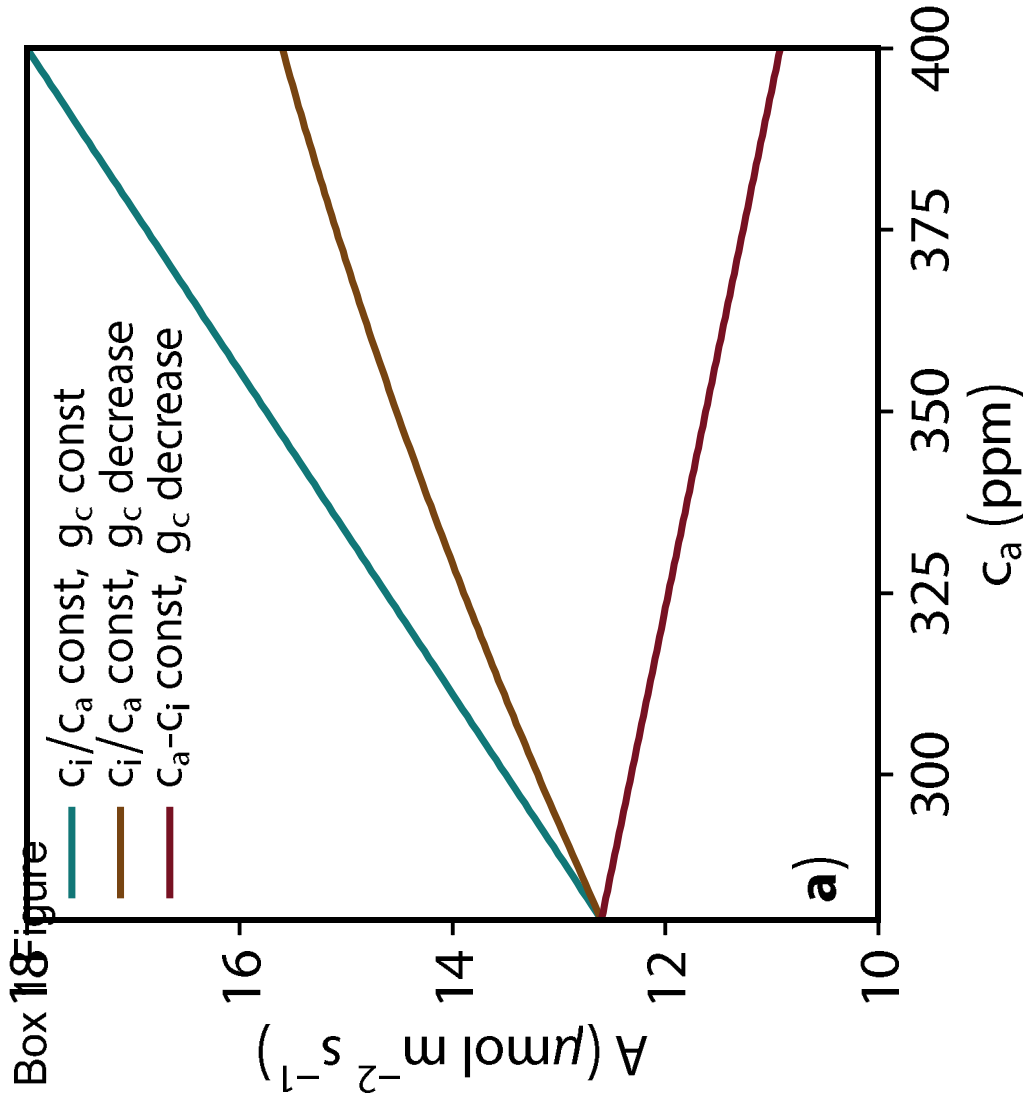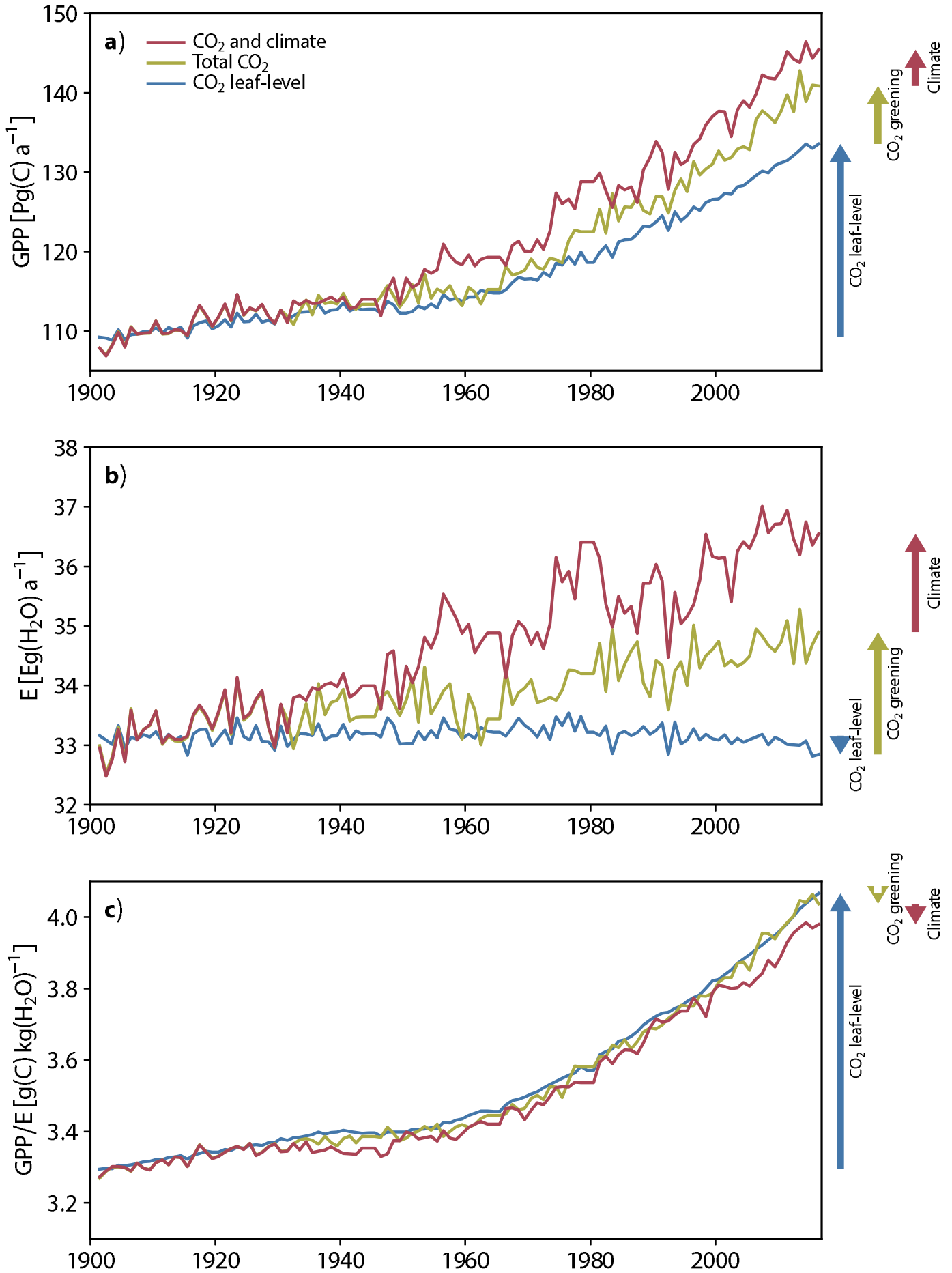
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Fig. 4

Box 1.8 Figure

a) Graph of A (μmol m^{-2} s^{-1}) versus c_a (ppm) with legend:
- c_i/c_a const, g_c const
- c_i/c_a const, g_c decrease
- $c_a - c_i$ const, g_c decrease

b) Graph of A/E [mmol(CO_2) mol(H_2O)$^{-1}$] versus c_a (ppm) with legend:
- c_i/c_a const, VPD const
- c_i/c_a const, VPD increase
- $c_a - c_i$ const, VPD increase

Figure 2

Figure 3

a) 12 tropical tree species

b) 9 subtropical tree species