

## Opinion

Robust Response of Terrestrial Plants to Rising CO<sub>2</sub>

Lucas A. Cernusak,<sup>1,\*</sup> Vanessa Haverd,<sup>2</sup> Oliver Brendel,<sup>3</sup> Didier Le Thiec,<sup>3</sup> Jean-Marc Guehl,<sup>3</sup> and Matthias Cuntz<sup>3</sup>

Human-caused CO<sub>2</sub> emissions over the past century have caused the climate of the Earth to warm and have directly impacted on the functioning of terrestrial plants. We examine the global response of terrestrial gross primary production (GPP) to the historic change in atmospheric CO<sub>2</sub>. The GPP of the terrestrial biosphere has increased steadily, keeping pace remarkably in proportion to the rise in atmospheric CO<sub>2</sub>. Water-use efficiency, namely the ratio of CO<sub>2</sub> uptake by photosynthesis to water loss by transpiration, has increased as a direct leaf-level effect of rising CO<sub>2</sub>. 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<sub>2</sub> and contemporary climate change.

### Rising Atmospheric CO<sub>2</sub> and Global Climate Change

Emissions of CO<sub>2</sub> associated with human industrial activity and land-use change over the past century have significantly impacted on global climate, causing global warming of about 1.0°C [1]. The anthropogenic CO<sub>2</sub> emission rate is continuing to increase, and the future rise in atmospheric CO<sub>2</sub> will undoubtedly lead to more climate change, including increases in the frequency of extreme climate events such as heatwaves, 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 accelerating accumulation of CO<sub>2</sub> in the atmosphere [4–6].

On the other hand, plants interact directly with atmospheric CO<sub>2</sub>, and they can potentially respond to rising atmospheric CO<sub>2</sub> concentrations by increasing photosynthetic rates and **water-use efficiency** (see [Glossary](#)) [7–10]. Water-use efficiency in this context is defined as the amount of CO<sub>2</sub> 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<sub>2</sub> fertilization is crucial for formulating effective mitigation and adaptation strategies [11].

At a global scale, there is currently an imbalance between the amount of CO<sub>2</sub> 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<sub>2</sub> that would otherwise result from anthropogenic CO<sub>2</sub> emissions. Predicting the future behaviour of the land carbon sink is one of the most important challenges in carbon cycle science, given the potential that feedbacks could accelerate the rate of future climate change [13]. This requires a thorough understanding of the process through which the terrestrial biosphere captures CO<sub>2</sub> – photosynthesis.

### Highlights

Global climate change caused by CO<sub>2</sub> emissions can stress terrestrial vegetation, potentially decreasing production. On the other hand, CO<sub>2</sub> interacts directly with plants, stimulating leaf-level photosynthesis and water-use efficiency.

The rise in atmospheric CO<sub>2</sub> concentration over the past century presents an opportunity for gauging the strength of the terrestrial biosphere response to these potential impacts.

Atmospheric proxy and model analysis both suggest that global terrestrial photosynthesis has increased in nearly constant proportion to the rise in atmospheric CO<sub>2</sub> 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.

<sup>1</sup>College of Science and Engineering, James Cook University, Cairns, QLD 4879, Australia

<sup>2</sup>Commonwealth Scientific and Industrial Research Organisation (CSIRO) Oceans and Atmosphere, Canberra, ACT 2601, Australia

<sup>3</sup>Université de Lorraine, Institut National de la Recherche Agronomique (INRA), AgroParisTech, Unité Mixte de Recherche Silva, 54000 Nancy, France

\*Correspondence: [lucas.cernusak@jcu.edu.au](mailto:lucas.cernusak@jcu.edu.au) (L.A. Cernusak).

## The Response of Terrestrial Gross Primary Production over the Past Century

**Gross primary production (GPP)** is the total amount of CO<sub>2</sub> absorbed by photosynthesis per unit time. Examining the GPP response to historic changes in atmospheric CO<sub>2</sub> can provide useful insight into how the terrestrial biosphere has responded to human-caused CO<sub>2</sub> emissions and global climate change so far. The concentration of atmospheric CO<sub>2</sub> 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 20th century. This >40% increase in atmospheric CO<sub>2</sub> concentration provides a global-scale experiment that has allowed scientists to assess the response of GPP to higher CO<sub>2</sub> levels.

Recently, a sulfur-containing analogue of CO<sub>2</sub> in the atmosphere, **carbonyl sulfide (COS)**, has been used to estimate the historical, proportional increase in global GPP over the past century [14]. COS in the atmosphere, from oceanic and anthropogenic sources, shows seasonal and diurnal cycles as well as a long-term trend that can be related to its flux into leaves when they are photosynthetically active [15–17]. Thus, it behaves similarly to CO<sub>2</sub> 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 complication of having simultaneous fluxes into and out of plants at the same time as occurs with CO<sub>2</sub>. The proportional increase in GPP from the year 1900 to 2013 based on the COS atmospheric budget was estimated to be  $31 \pm 5\%$  [14], which is directly proportional to the increase in atmospheric CO<sub>2</sub> concentration (Figure 1).

This suggests that the photosynthetic activity of the terrestrial biosphere has kept pace remarkably with the historic rise in atmospheric CO<sub>2</sub> concentration and its associated climate change. To better understand this intriguing result, we applied the community atmosphere–biosphere land exchange model (CABLE) to the historic time period of interest [18]. This model was recently shown to outperform a range of terrestrial biosphere models in its ability to correctly simulate the 20th century increase in global GPP as deduced from the COS atmospheric constraint (V. Haverd *et al.*, unpublished). The analysis by CABLE suggests that the largest proportion of GPP growth resulted from a direct effect of CO<sub>2</sub> fertilization on photosynthesis rates (Figure 2A), and that there were additional effects associated with greening – an increase in leaf area – which took place mainly in semi-arid regions, as well as with climate change. In gauging the strength of this response of GPP in the terrestrial biosphere to rising CO<sub>2</sub> and climate change, we find that a very simplified mathematical description, as shown in Box 1, can help to place it in context.

### Contextualizing the GPP Response

Taking a reductionist approach, the response of the terrestrial biosphere to 20th century climate change can be abstracted to that of a single leaf. By replacing  $A$  (the net rate of CO<sub>2</sub> assimilation by photosynthesis) in Box 1 Equation II with GPP, one then obtains the surprising result that the globally scaled term  $g_c(1 - c_i/c_a)$  would need to have remained approximately constant to explain the observed increase in GPP over the past century, because GPP has increased in nearly constant proportion to the increase in  $c_a$  (Figure 1 and Box 1). Such an abstraction ignores several processes that are known to be important to photosynthesis, for example, mesophyll conductance [25], but we note that the overall thrust of our argument would not change if these processes were also taken into account.

The  $c_i/c_a$  is the **intercellular to ambient CO<sub>2</sub> concentration ratio** during photosynthesis. Because photosynthetic enzymes consume CO<sub>2</sub> inside the leaf, the concentration of CO<sub>2</sub> in the air spaces inside leaves,  $c_i$ , decreases below the ambient concentration,  $c_a$ . The proportional reduction in  $c_i$  relative to  $c_a$  can be considered to be a gas exchange set-point, a diagnostic feature of the photosynthetic behaviour of terrestrial plants [26]. Assessing the variation in this

### Glossary

#### Carbon isotope discrimination

( $\Delta^{13}\text{C}$ ): the extent to which the  $^{13}\text{C}/^{12}\text{C}$  ratio of photosynthetically assimilated carbon differs from that of the atmospheric CO<sub>2</sub> which provided the substrate for photosynthesis.

**Carbonyl sulfide (COS)**: a trace gas in the atmosphere which is destroyed by enzymes inside leaves that are active during photosynthesis. For this reason COS consumption by leaves can be linked to CO<sub>2</sub> assimilation by photosynthesis.

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

#### Intercellular to ambient CO<sub>2</sub>

**concentration ratio ( $c_i/c_a$ )**: the ratio of the CO<sub>2</sub> concentration in the intercellular air spaces inside a leaf ( $c_i$ ) to that in the atmosphere outside the leaf ( $c_a$ ). It is a measure of the balance between the supply of CO<sub>2</sub> by stomata and its consumption by photosynthesis.

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

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

#### Leaf-to-air water vapour

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

**Stomatal conductance ( $g_s, g_c$ )**: the rate of CO<sub>2</sub> diffusion into or water vapour diffusion out of a leaf relative to the concentration gradient driving diffusion. It is controlled by the number, size, and openness of stomatal pores. The stomatal conductance to water vapour ( $g_s$ ) is 1.6-fold that for CO<sub>2</sub> ( $g_c$ ) owing to the different sizes of the molecules.

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

## Box 1. Plant Physiological Theory

Plant physiological theory predicts that photosynthesis and water-use efficiency should increase as the CO<sub>2</sub> concentration surrounding a leaf increases [7,19,20]. Although simple in formulation, this theory can explain some of the most impactful changes in the functioning of terrestrial plants in response to rising atmospheric CO<sub>2</sub> (Figure 1). Fick's law of diffusion provides one basis for a mathematical description of photosynthesis:

$$A = g_c(c_a - c_i) \quad \text{[I]}$$

where  $A$  is the net rate of CO<sub>2</sub> assimilation by photosynthesis,  $g_c$  is the stomatal conductance to CO<sub>2</sub>,  $c_a$  is the CO<sub>2</sub> concentration in the air outside the leaf, and  $c_i$  is the CO<sub>2</sub> concentration in the leaf intercellular air spaces. This equation can also be written as:

$$A = c_a g_c \left(1 - \frac{c_i}{c_a}\right) \quad \text{[II]}$$

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

$$E = g_s(w_i - w_a) \quad \text{[III]}$$

where  $g_s$  is stomatal conductance to water vapour, which is typically taken as  $1.6g_c$  because H<sub>2</sub>O molecules diffuse faster than CO<sub>2</sub>. The  $w_i$  is the water vapour concentration in the intercellular air spaces inside the leaf, and  $w_a$  is that in the air outside the leaf. Dividing Equation II by Equation III yields an expression for water-use efficiency ( $A/E$ ):

$$\frac{A}{E} = \frac{c_a \left(1 - \frac{c_i}{c_a}\right)}{1.6(w_i - w_a)} \quad \text{[IV]}$$

Equation IV shows that there are two processes to modify the response of  $A/E$  to  $c_a$ : these are  $c_i/c_a$  and the leaf-to-air water vapour concentration difference,  $w_i - w_a$ .

Time-integrated estimates of  $c_i/c_a$  can be obtained by measuring carbon isotope discrimination ( $\Delta^{13}\text{C}$ ) with respect to atmospheric CO<sub>2</sub> in C<sub>3</sub> plants [21–23]. The equation relating the two is:

$$\Delta^{13}\text{C} = a + (b-a) \frac{c_i}{c_a} \quad \text{[V]}$$

where  $a$  is the <sup>13</sup>C/<sup>12</sup>C fractionation that occurs during diffusion of CO<sub>2</sub> through stomata (4.4‰) and  $b$  is the fractionation that occurs during carboxylation by Rubisco (27‰). The  $\Delta^{13}\text{C}$  can be measured in plant dry mass and provides an integrated record of  $c_i/c_a$  over the period during which the tissue was formed [24].

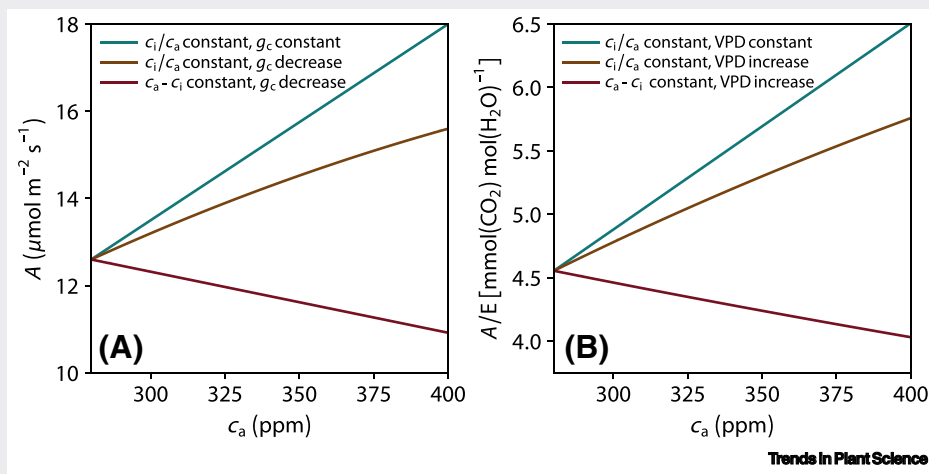


Figure 1. Three Possible Scenarios That Could Occur for the Photosynthesis Rate and the Water-Use Efficiency of a Leaf in Response to Rising Atmospheric CO<sub>2</sub> Concentration ( $c_a$ ). In (A) the maximal response occurs when both  $c_i/c_a$  and stomatal conductance do not change in response to rising  $c_a$ . In (B) the maximal response occurs when  $c_i/c_a$  and  $w_i - w_a$  do not change in response to rising  $c_a$ . Abbreviation: VPD, vapour pressure deficit.

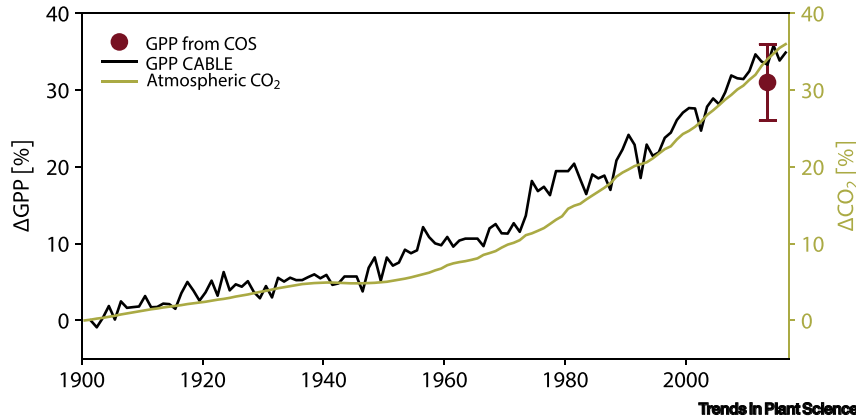


Figure 1. Proportional Changes in Gross Primary Production (GPP) from 1900 to 2013 Inferred from Carbonyl Sulfide (COS) in the Atmosphere (Red Dot), as Predicted by a Global Land-Surface model, CABLE [18] (Black Line). The error bars on the red dot represent the 95% confidence interval around the COS-based estimate of the proportional change in GPP [14]. The gold line shows the proportional increase in atmospheric CO<sub>2</sub> concentration over the same time-period.

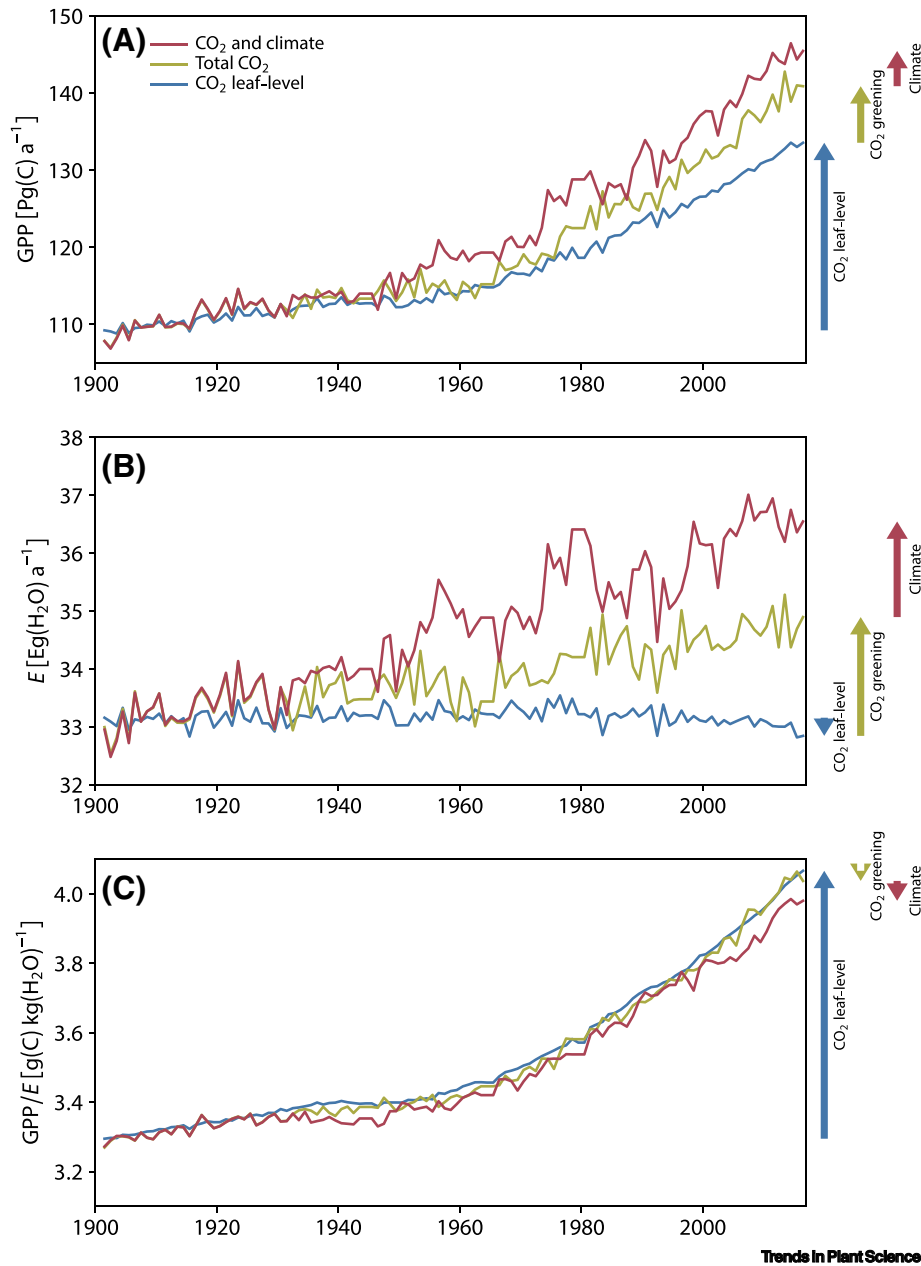
attribute has been greatly facilitated by the relationship between **carbon isotope discrimination ( $\Delta^{13}\text{C}$ )** and  $c_i/c_a$  in plants which use the C<sub>3</sub> photosynthetic pathway (Box 1). Plants using the C<sub>3</sub> photosynthetic pathway make up most of the biomass in the terrestrial biosphere [27].

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

Although less common, analyses of  $\Delta^{13}\text{C}$  in herbarium leaves can also be used to test whether  $c_i/c_a$  has changed over the past century. As with tree ring results, these studies are consistent with the idea of a relatively constant  $c_i/c_a$  in response to rising atmospheric CO<sub>2</sub> concentration over the 20th century [38–40].

Recent analysis of the  $^{13}\text{C}/^{12}\text{C}$  ratio in atmospheric CO<sub>2</sub> over the past century has also corroborated the trend of an approximately constant  $c_i/c_a$  in leaves of terrestrial plants as the atmospheric CO<sub>2</sub> concentration increased [41]. This led the authors to conclude that globally,  $A/g_c$  of land plants [equivalent to  $c_a(1 - c_i/c_a)$ ] has increased in nearly constant proportion to the increase in  $c_a$ .

Assuming, as the above evidence suggests, that  $c_i/c_a$  has changed little in land plants in response to rising  $c_a$ , Equation II in Box 1 indicates that the global, big-leaf analogy for **stomatal conductance ( $g_s, g_c$ )** must also have changed little. This is surprising because stomatal conductance is known to decrease in response to increasing  $c_a$  [10,20,42–44]. The response can involve both morphological and physiological components [19]. For example, maximum stomatal conductance was shown to decrease across a range of species as a result of decreases in both stomatal density and stomatal pore size [45–49], as shown in Figure 3B for a range of subtropical tree



**Figure 2. Changes in Gross Primary Production (GPP) and Global Transpiration with Time.** (A) Attribution of changes in GPP of the terrestrial biosphere to leaf-level stimulation of photosynthesis, increasing leaf area (greening), and changing climate, as simulated by the land-surface model CABLE [18]. (B) Changes in global transpiration,  $E$ , with the same attributions as in panel A. (C) Changes in global water-use efficiency, calculated as global GPP divided by global transpiration, with attributions as described for panel A.

species over the past century [45]. In addition, stomatal conductance is known to decrease in response to CO<sub>2</sub> in short-term exposure experiments [50].

If  $A$  is replaced with global annual GPP in Equation II in Box 1, then  $g_c$  becomes the global conductance to CO<sub>2</sub> per unit ground area summed annually rather than being an instantaneous

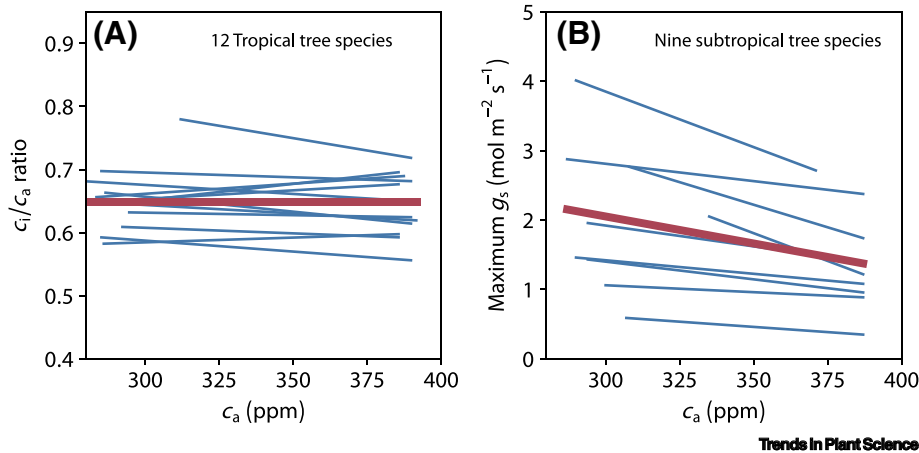


Figure 3. Examples of Trends in  $c_i/c_a$  Inferred from Carbon Isotope Ratios of Tree Rings (A) and Maximum  $g_s$  Calculated from Leaf Anatomical Dimensions of Stomatal Density and Stomatal Pore Size (B). Data in panel A are from van der Sleen *et al.* [29] and those in panel B are from Lammertsma *et al.* [45]. The blue lines in each panel show individual species responses and the red lines show the mean responses of all species. Abbreviations:  $c_a$ ,  $\text{CO}_2$  concentration in the air outside the leaf;  $c_i$ ,  $\text{CO}_2$  concentration in the leaf intercellular air spaces;  $g_s$ , stomatal conductance to water vapour.

conductance per unit leaf area. The result of constant global annual conductance then suggests that the total leaf area of terrestrial plants and the average length of the growing season have increased in such a way as to offset the likely reduction in stomatal conductance per unit leaf area and time caused by increasing  $c_a$  (Figure 3B). This is consistent with remotely sensed observations of greening of the global land surface [51–53], observed increases in growing-season length especially in the northern hemisphere [54,55], and with the CABLE simulations (Figure 2A). These observations and modelling analyses suggest that  $\text{CO}_2$  fertilization has driven increases in **leaf area index (LAI)** in the tropics, whereas global warming has driven increases in LAI and growing-season length in high-latitude ecosystems.

### Water-Use Efficiency Has Risen Markedly

The term  $A/g_s$  is often referred to as intrinsic water-use efficiency because it does not depend on the **leaf-to-air water vapour concentration difference ( $w_i - w_a$ )**. As can be seen from Equation II in Box 1, if  $c_i/c_a$  remains constant in response to increasing  $c_a$ , then  $A/g_s$  will increase in constant proportion to the increase in  $c_a$ . However, an important question arises as to how the actual water-use efficiency  $A/E$  has responded because  $w_i - w_a$  could also have increased with global warming. As seen in Equation IV in Box 1, an increase in  $w_i - w_a$  will cause a reduction in  $A/E$ . The  $w_i - w_a$  might have increased for two reasons. First, air vapour pressure deficit is likely to increase with global warming owing to the potential for warmer air to hold more water vapour. Second, the difference between leaf temperature and air temperature is also likely to increase if stomata close somewhat in response to rising  $c_a$  owing to reduced evaporative cooling of the leaf by transpiration. Thus, the response of  $A/E$  to rising  $c_a$  depends on the competing effects of increasing  $A/g_s$  and increasing  $w_i - w_a$ .

We used the CABLE model to gain insight into this question. The simulation suggested that the increase in global transpiration with the 20th century rise in  $c_a$  and associated global warming was relatively modest (Figure 2B). Thus GPP/ $E$ , the ratio of global gross primary production to global transpiration, showed a marked increase according to the model simulation (Figure 2C). This is consistent with other recent model analyses which showed similarly modest impacts of



CO<sub>2</sub>-induced global warming on transpiration, and therefore strong impacts on *A/E* or its global analogue *GPP/E* [9,42,56]. Evapotranspiration, the sum of transpiration and soil evaporation, decreased by ~2% over the simulated time-period, such that if water-use efficiency were expressed as *GPP* divided by evapotranspiration, then the increasing trend with time would have been even slightly stronger than that for *GPP/E*.

Direct measurements of ecosystem-level CO<sub>2</sub> and water vapour fluxes through eddy covariance also show strong increases in ecosystem water-use efficiency over the past three decades [9, 57–60]. In addition, consistent with results in Figure 2, a recent global analysis, which combined ground-based and remotely sensed land and atmospheric observations, showed that increasing water-use efficiency stimulated *GPP* directly, and also led to increasing leaf area index, accounting for further gains in *GPP* [58].

### Concluding Remarks and Future Perspectives

Recent analyses suggest that the terrestrial biosphere has responded to anthropogenic CO<sub>2</sub> emissions over the past century with a maximal increase in photosynthetic activity that proportionally matched the increase in atmospheric CO<sub>2</sub> concentration. This partly resulted from a marked increase in leaf-level photosynthesis and water-use efficiency, which stimulated increases in leaf area in water-limited environments, while rising temperatures lengthened growing seasons at high latitudes. The increases in global leaf area and in growing-season length approximately offset the impact of decreasing stomatal conductance at the leaf level, such that the global conductance per unit ground area summed annually remained nearly constant.

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

An important outstanding question that emerges from our analysis concerns whether the observed trend for *GPP* to increase in nearly constant proportion to *c<sub>a</sub>* will continue with future increases in *c<sub>a</sub>*. The present-day value of *c<sub>a</sub>* is about 410 ppm, and this could double by the end of the 21st century. Over this range, it seems likely that *GPP* growth will slow owing to saturating photosynthesis, nutrient limitations, or leaf area reaching a maximum per unit ground area. Knowing when the slowing will start and to what extent it will depress *GPP* growth will be crucial for evaluations of carbon cycle feedbacks to future global warming.

A second important question concerns the extent to which increases in *GPP* will stimulate net primary production (*NPP*), the response that can most effectively produce a terrestrial carbon sink. Some CO<sub>2</sub> enrichment experiments have indicated that nutrient and water availability limit the *NPP* response to elevated CO<sub>2</sub> more than the *GPP* response [63–67]. In these cases the extra carbon captured by photosynthesis is rapidly cycled back to the atmosphere through microbial respiration of root exudates or ephemeral plant parts such as leaves, fine roots, and mycorrhizae [68–70]. Given these experimental results, it could be expected that the land carbon sink will not increase proportionally with *GPP* growth in response to rising *c<sub>a</sub>*.

Global climate change caused by CO<sub>2</sub> emissions carries tremendous risks for human society. In this Opinion, we argue that terrestrial plants have responded vigorously to the historic increase in atmospheric CO<sub>2</sub>, and that adverse impacts of global climate change on terrestrial plant production have been overshadowed by the positive effects of CO<sub>2</sub> fertilization at the global scale.

### Outstanding Questions

Can terrestrial plants continue to coordinate investment of nutrient resources into different components of the photosynthetic process such that CO<sub>2</sub> assimilation rates continue to increase as ambient CO<sub>2</sub> concentration continues to rise?

Will availability of mineral nutrients become progressively limiting to photosynthesis as atmospheric CO<sub>2</sub> concentrations become less limiting?

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

How is land-use change impacting on the trajectory of the photosynthetic response of the terrestrial biosphere to rising CO<sub>2</sub> and climate change?

Will the response of *NPP* to rising CO<sub>2</sub> slow before that of *GPP*, diminishing the growth of the land carbon sink more quickly than the growth of terrestrial photosynthesis?

However, this should not be interpreted as lessening the urgency with which global climate change should be addressed by drastically and rapidly reducing human-caused CO<sub>2</sub> emissions [2] (see Outstanding Questions).

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