Plants, CO_2 and photosynthesis in the 21st century

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Human activity in the last 200 years has led to a marked increase in the level of CO_2 in the atmosphere. Plants sense increases in CO_2 levels and initially respond with an increase in photosynthetic rate, which may then slow as the plant adapts. This increase in photosynthetic rate may account in part for the 'disappearance' of an estimated 1.8 gigatons of carbon per year.

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Introduction

Inorganic carbon is the basis for organic life on earth. Plants are the central link in this transformation, converting inorganic carbon dioxide (CO_2) in the atmosphere to organic carbon in the biosphere by photosynthesis. As the primary biological process within the global carbon cycle, photosynthesis also directly links changes in the earth's atmosphere caused by humans to the biological functioning of both natural and agricultural ecosystems. In this review we will examine the effects of rising atmospheric CO_2 partial pressure ($(pCO_2)_a$) on the process of photosynthesis. We describe the critical components of photosynthesis that ultimately control atmosphere–biosphere interactions, explain how these processes may be altered by the rise in $(pCO_2)_a$ due to human activity, and speculate on how these changes may affect the global carbon cycle of the 21st century and beyond.

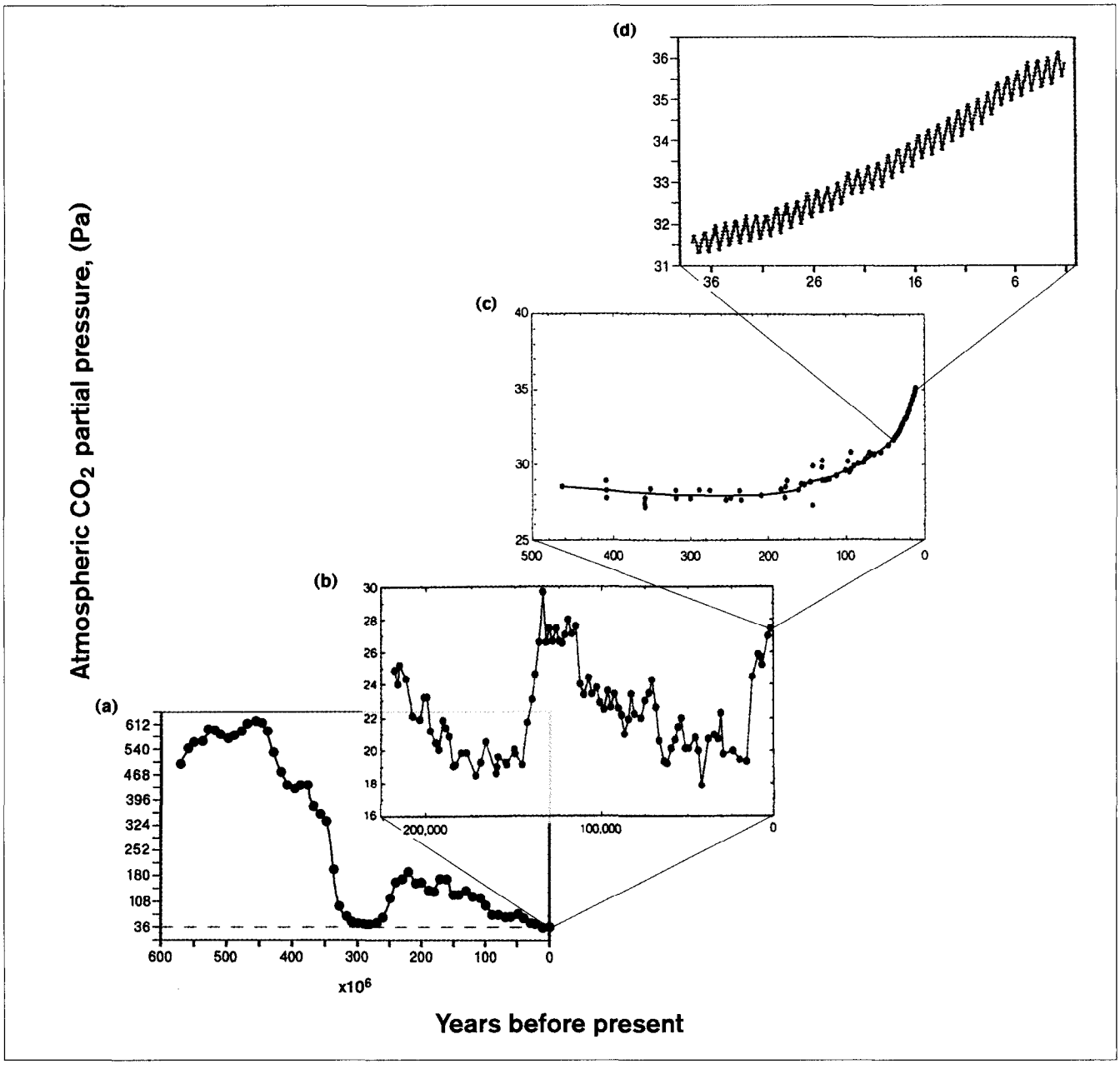
CO_2 in the atmosphere

Over geological time, it is mineral weathering that ultimately controls $(pCO_2)_a$. The ocean/atmosphere system is an important component of the global carbon cycle, but has both a very fast response time to changes in CO_2 partial pressure and a very low capacity to store carbon relative to rocks [1]; it consequently affects $(pCO_2)_a$ only over relatively short periods of time (centuries).

Changes in $(pCO_2)_a$ are not a new phenomenon. Although no direct data exist, models (e.g., [1]) suggest that, at certain times over the last 550 million years, $(pCO_2)_a$ may have been nearly 20 times the current level (i.e., as high as 600 Pa; the current $(pCO_2)_a$ is 36 Pa, see Fig. 1a). On a shorter time scale (the last two glacial cycles), direct measurements of air trapped in bubbles within ice-cores from Antarctica reveal fluctuations of 12 Pa over the last 220 000 years [2] (Fig. 1b). Over the short term, the picture is different; bubbles from Greenland ice-cores, which provide a record of $(pCO_2)_a$ during the past five centuries, show that $(pCO_2)_a$ is relatively stable at ~27 Pa [3], beginning to rise only after the industrial revolution, when human-caused CO_2 release became significant (Fig. 1c). Direct measurements of $(pCO_2)_a$ from the top of Mauna Loa, Hawaii [4] (Fig. 1d), which started in 1957, document both seasonal changes in $(pCO_2)_a$ induced by biological activity (primarily northern hemisphere photosynthesis) and increases in $(pCO_2)_a$ resulting from human activity (primarily fossil fuel combustion and land use changes such as deforestation).

Several features of the $(pCO_2)_a$ record are important in the context of this review. First, over geological time

Figure 1



Atmospheric CO_2 levels over geological time. **(a)** Partial pressure for the last 600,000,000 years, modeled from the geochemical global carbon cycle of Berner [1] (estimated error is ± 50 %). **(b)** Atmospheric CO_2 during the last two major glacial periods (220,000 years) measured from ice core bubbles [2]. **(c)** CO_2 during the last 500 years, also measured from ice core bubbles [3]. **(d)** Direct atmospheric measurements of CO_2 levels from the top of Mauna Loa volcano in Hawaii made since 1957 [4]. The dips correspond to summer in the Northern hemisphere.

$(pCO_2)_a$ has fluctuated dramatically. Second, land plants evolved during periods of relatively high $(pCO_2)_a$ (plants migrated to land ~400 x 10^6 years ago, when the $(pCO_2)_a$ level was ~10-fold higher). Third, the seasonal fluctuations evident in Figure 1d indicate that photosynthesis by terrestrial vegetation has a strong influence on $(pCO_2)_a$ on an annual time scale. Finally, changes in the global carbon cycle due to human activity have caused a substantial increase in $(pCO_2)_a$; the level of atmospheric CO_2 has risen 30 % since the industrial revolution (starting 200 years ago; Fig. 1c) and continues rising unabated. This global increase in $(pCO_2)_a$ is occurring much faster than plants are capable of genetically adapting to the change, and will alter the functional balance of photosynthetic reactions. It will also probably increase the influence of plants on the global carbon cycle.

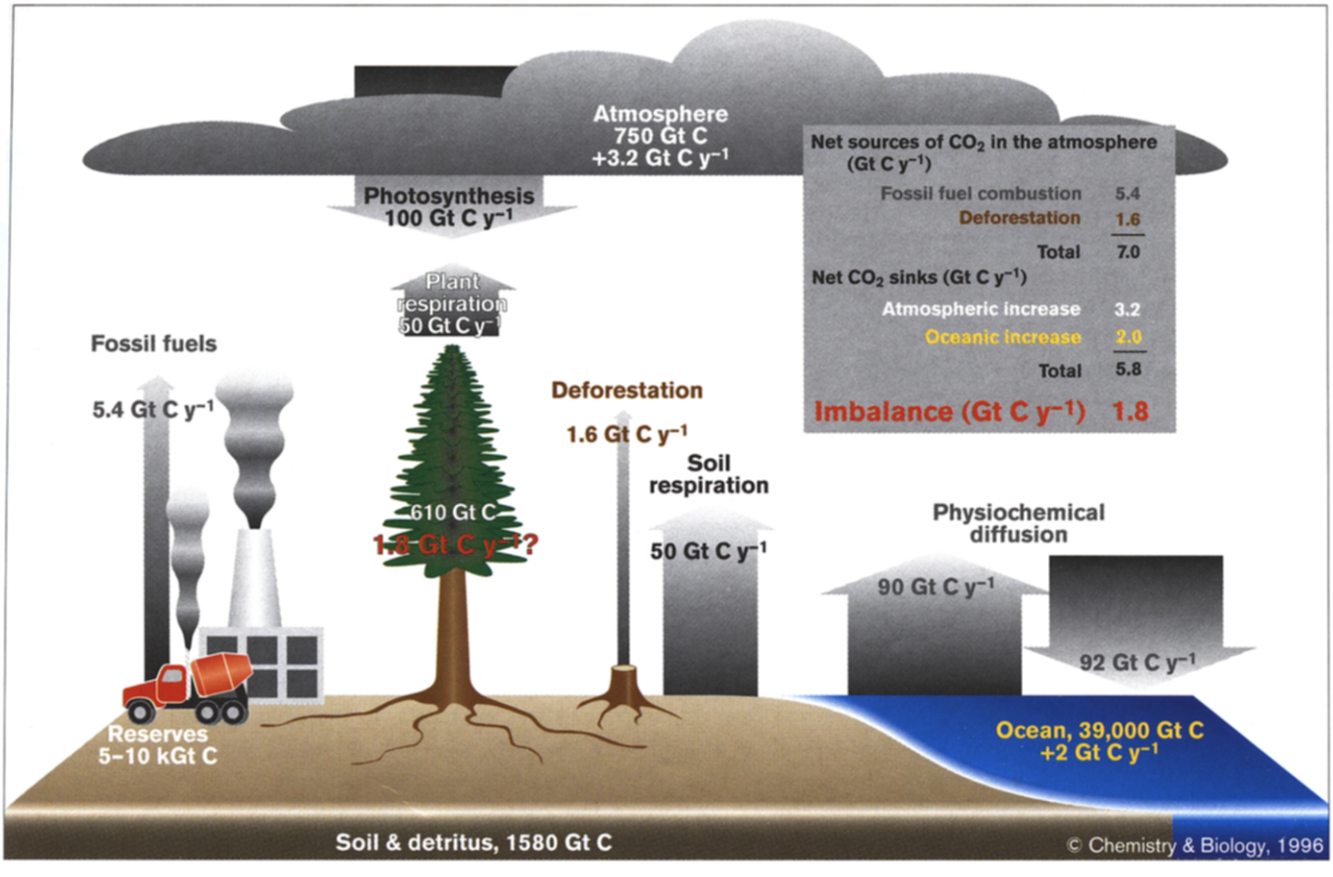
The global carbon cycle

Our representation of the contemporary global carbon cycle (Fig. 2) identifies the major pools and fluxes of elemental carbon, estimated in gigatons of carbon (Gt C) for the pools and Gt C y^{-1} for the fluxes (from [5–7]). Pools and fluxes relevant to geological carbon cycling are not illustrated (i.e., rock weathering). The only significant flux of CO_2 out of the atmosphere that is not governed strictly by physical factors (e.g., physiochemical diffusion into the oceans) is that resulting from photosynthesis (represented by the tree).

As the inset to Figure 2 shows, our best estimates of carbon uptake and release are not balanced. Photosynthetic carbon uptake by land plants may amount to as much as 100 Gt C y^{-1} [6], most of which is eventually returned to the atmosphere by the respiration of plants and soil biota. The known net sources of $(pCO_2)_a$ include ~5.4 Gt C y^{-1} from the combustion of fossil fuels and ~1.6 Gt C y^{-1} from changes in land use (principally deforestation). If we balance the current estimates for carbon sources (estimated to be 7 Gt C y^{-1}) against the known carbon sinks (5.2 Gt C y^{-1}; 3.2 Gt C y^{-1} is the measured increase in the CO_2 content of the atmosphere and ~2.0 Gt C y^{-1} is estimated to be entering the worlds oceans), we cannot account for ~1.8 Gt C y^{-1}. In other words, an amount of carbon equivalent to 56 % of the annual increment to the atmosphere is going into an as yet unidentified sink (the so-called 'missing sink'; see box, Fig. 2). It has been proposed that the amount of carbon fixation by photosynthesis and/or the carbon residence time in terrestrial vegetation has been underestimated. Carbon sequestration in the form of northern hemisphere forest re-growth, plant growth stimulation by nitrogen deposition from natural and anthropogenic sources, and most importantly, a direct 'fertilization' (i.e., stimulation) of plant growth by elevated $(pCO_2)_a$ may account for this missing sink.

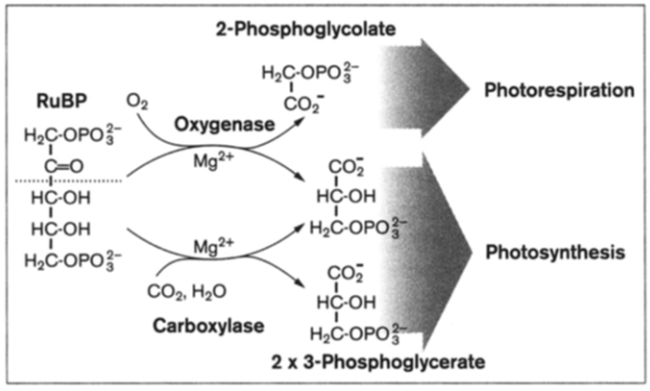
To assess whether terrestrial vegetation can account for the missing carbon sink, we must first answer the question of whether plant growth is stimulated by elevated $(pCO_2)_a$. This could be accomplished in one of three general ways. Photosynthetic carbon fixation could increase, carbon losses (e.g., respiration, root exudation,

Figure 2



The contemporary global carbon cycle. All estimates are in Gt C (pools) and Gt C y^{-1} (fluxes). Arrow thickness is roughly proportional to the magnitude of each carbon flux. The box shows the calculation of the imbalance between net sources of CO_2 and net CO_2 sinks, which may be explained by an underestimation of the amount of carbon that is sequestered due to plant growth. Estimates from [5–7].

Figure 3



Reactions catalyzed by ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) [9]. The carboxylase activity catalyzes the addition of CO_2 to ribulose 1,5-bisphosphate (RuBP) to form two molecules of 3-phosphoglycerate, which are used to make triose phosphates, then carbohydrates. The competing oxygenase reaction yields one molecule of 2-phosphoglycolate and one molecule of 3-phosphoglycerate.

volatilization of hydrocarbons) could decrease, or a combination of both could occur. Although the picture is far from clear at present our existing knowledge of plant responses to elevated CO_2 indicates that plant growth is stimulated, and that the primary and most significant mechanism for this is an increase in the rate of photosynthetic CO_2 uptake. This increase is a result of the biochemical characteristics of the photosynthetic CO_2-fixing enzyme, ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco). The CO_2 response of this enzyme, the most abundant protein in the biosphere [8], initiates a cascade of molecular events culminating in a number of apparently diverse plant responses to growth in elevated $(pCO_2)_a$.

CO_2 and the biochemistry of photosynthesis

In the first step of the photosynthetic carbon reduction (Calvin) cycle, Rubisco catalyzes the carboxylation of the five-carbon sugar phosphate ribulose-1,5-bisphosphate (RuBP) by atmospheric CO_2 to yield two molecules of the three-carbon (C_3) organic acid 3-phosphoglycerate (Fig. 3) [9]. In C_3 plants (~95 % of all higher plant species) elevated $(pCO_2)_a$ substantially stimulates the rate of this reaction in the very short term (within minutes), because Rubisco operates below its K_M for CO_2 and at about 25 % of V_{max} at present day $(pCO_2)_a$ [10,11]. Rubisco also catalyzes a competitive reaction with O_2, the oxygenation of RuBP, forming one molecule of 2-phosphoglycolate and one molecule of 3-phosphoglycerate. This is the initial reaction of the energy-consuming process of photorespiration, which reduces potential carbon assimilation by as much as 40 % in C_3 species at the present $(pCO_2)_a$ and $(pO_2)_a$ [12]. The difference in the affinity of Rubisco for its two gaseous substrates (the K_M for O_2 is 700 times lower than that for CO_2) dictates that increases in $(pCO_2)_a$ will substantially reduce O_2 uptake and photorespiration relative to CO_2 uptake.

The properties of Rubisco thus cause a large and consistent short-term stimulation of photosynthesis, which is observed when C_3 plants are initially exposed to high CO_2. At high CO_2 partial pressure, it is rarely, if ever, the capacity of Rubisco to fix atmospheric CO_2 that limits the overall rate of photosynthesis. At higher pCO_2 the rate of photosynthesis becomes limited by the capacity to regenerate RuBP. The upper limit on the rate of CO_2 fixation probably results from a finite capacity of the synthetic reactions to use the triose phosphate produced by the Calvin cycle; these downstream reactions release inorganic phosphate (P_i), which is required for subsequent ATP synthesis and RuBP regeneration, from phosphorylated intermediates [13–16]. Under these conditions, additional CO_2 has little effect on the overall rate of CO_2 assimilation, and photosynthesis is described as 'P_i limited' or 'triose-phosphate-use limited' [13]. In such cases, Rubisco activity is typically down-regulated so that it remains balanced with the limiting process (either P_i or RuBP regeneration). Reduction in Rubisco activity has been observed following even short-term exposure to high CO_2, and is accomplished by decarbamylation of the enzyme [17,18]. Similarly, when the capacity to regenerate P_i limits photosynthesis, the rate of photosynthetic electron transport is also down-regulated [19].

This suite of responses to elevated CO_2 levels reflects short-term regulatory control within the photosynthetic apparatus. It is thought to coordinate the rate of RuBP production with the rate of its consumption, the rate of triose-phosphate production with the rate of its use for carbohydrate synthesis, and the rate of energy input to the system with the overall rate of carbon output [18,20,21]. This feedback regulation of photosynthesis is not an efficient long-term solution to the imbalance between carbon acquisition and use resulting from an accelerated rate of carbon input at elevated $(pCO_2)_a$, however. Nitrogen-rich components of the photosynthetic apparatus, in particular Rubisco, are simply being 'turned off' rather than being reused to enhance other more rate-limiting processes [11,19]. Because nitrogen is such a limiting resource for plant growth, longer-term regulation of photosynthesis at elevated atmospheric CO_2 should ideally include adjustment of the level of components of the photosynthetic apparatus, in particular Rubisco, to match the growth-limiting process (e.g., carbohydrate use) if the plant is to maximize nitrogen-use efficiency.

CO_2 and the physiology of photosynthesis

The biochemical regulation of photosynthesis can be assessed through physiological measurements of leaf-level photosynthetic responses to short-term changes in intercellular pCO_2 (C_i) under steady-state conditions of

saturating light (Fig. 4a) [22]. Gas-exhange-based determinations of the rate of photosynthesis versus intracellular pCO_2 ($A:C_i$ response) in C_3 species can provide important information about the extent to which photosynthesis can be Rubisco-, RuBP-regeneration-, or P_i-limited [11,13,23,24]. Changes in the initial slope of the $A:C_i$ response at low CO_2 concentrations are a consequence of a change in the activity and/or content of Rubisco (Fig. 4a). Changes in the $A:C_i$ response and the sensitivity of CO_2 assimilation to oxygen ($A:O_2$) at high CO_2 concentrations can indicate changes in the extent to which RuBP-regeneration capacity and/or P_i availability limit photosynthesis (Fig. 4a). The actual photosynthetic rate at any given C_i is the minimum rate caused by one of these three potential limitations.

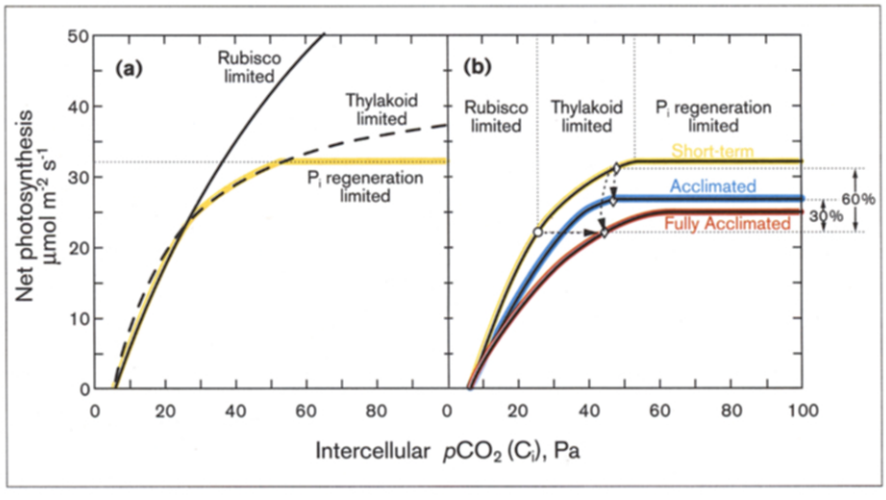
During short-term fluctuations in $(pCO_2)_a$ (minutes to hours), the photosynthetic response proceeds along the curve determined by the regulatory processes (Fig. 4b, yellow line), perhaps increasing by 10 to 100 % when the $(pCO_2)_a$ is raised from 35 to 70 Pa [25]. Many species do not maintain this initial high rate of photosynthesis in response to elevated CO_2, however [18,26–33]. For example, the 52 % average initial stimulation of photosynthesis reported by Cure and Acock [34] decreased to an average of 29 % after long-term exposure to high CO_2 (Fig. 4b, acclimated; blue curve). Over a period of days to weeks of growth in elevated $(pCO_2)_a$, this 'acclimation' response may in some species be substantial enough that the photosynthetic rates of plants grown and measured in elevated CO_2 (70 Pa) become equal to those of their ambient-CO_2-grown counterparts measured under their growth conditions (35 Pa; Fig. 4b, fully acclimated; red curve) [35]. In general, CO_2 assimilation rates for plants growing in high CO_2 are higher, or at least equal to, those of plants growing in ambient levels of CO_2; however, they are lower than the assimilation rates that would be predicted from the short-term $A:C_i$ response [36]. Down-regulation of the $A:C_i$ response has also been observed in some [37,38], but not all [39], natural and artificial ecosystems.

The long-term (days to weeks) response of photosynthetic activity to elevated $(pCO_2)_a$ can be substantially influenced by a variety of factors. The species of plant studied, the relationship between sources of and sinks for carbon, nitrogen and water availability, the developmental stage of the plant, age, reproductive status and rooting volume can all affect the response to elevated $(pCO_2)_a$. We propose that the apparently diverse responses to growth at elevated CO_2 are the result of a common control mechanism in all species, probably at the level of gene transcription. This mechanism is presumably triggered by a biochemical signal (probably the level of cytosolic glucose) that is influenced by environmental, genetic and/or developmental factors. One of the great challenges in understanding the CO_2 response in plants is to determine this control mechanism and the signal transduction pathway involved. The details that have been elucidated thus far are discussed below.

A model to explain the response to CO_2

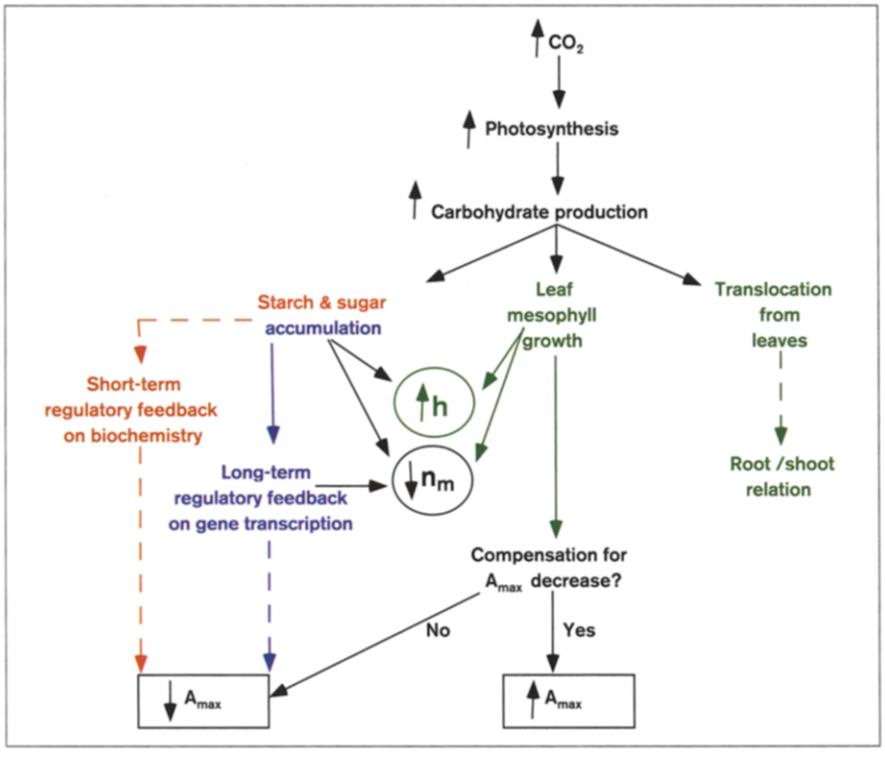
It is difficult to predict photosynthetic responses to growth in elevated CO_2 because of the variety of reported responses and the multitude of environmental and biochemical factors involved. Recently, Luo *et al.* [40] proposed a model that predicts photosynthetic responses

Figure 4



The photosynthetic rate increases in response to elevated $(pCO_2)_a$, but this increase can be modulated by acclimation. **(a)** Photosynthetic response to intercellular CO_2 partial pressure (C_i), modeled assuming three single limitations. The three potentially limiting steps are, Rubisco capacity (solid), thylakoid-dependent RuBP regeneration (long dash) and P_i regeneration (short dash). The photosynthetic rate at any given C_i is the minimum of these three potential limitations (yellow). **(b)** The yellow curve, reproduced from panel (a), indicates the short-term response to increased CO_2 levels; a 60 % increase in net photosynthetic rate when ambient CO_2 levels are doubled is typical. The diamond represents the net photosynthetic rate and C_i when ambient CO_2 is raised to 70 Pa for a brief period from the normal ambient level of 35 Pa (circle). Two longer-term responses are also depicted: an acclimated response (blue), which typically results in a 30 % decrease in the net photosynthetic rate compared to the short-term response (yellow), and a fully acclimated response (red), where the net photosynthetic rates of plants grown and measured at elevated CO_2 (70 Pa) are equal to those of plants grown and measured at ambient CO_2 (35 Pa). Modified from [25].

Figure 5



A model to predict photosynthetic responses to elevated CO_2. The model assumes that the initial response to elevated CO_2 is an increase in the net photosynthetic rate (as in Fig. 4), leading to an increase in photosynthetic products (carbohydrates) that can then feed back to influence the net photosynthetic rate. A pathway for short-term regulation of photosynthesis resulting from a limitation in P_i regeneration (see Figs 4,6) is in red and long-term regulation resulting from a change in gene transcription is in blue. Circled symbols (h = leaf mass per unit area and n_m = nitrogen per unit area) are model inputs, whereas the boxed symbols (A_{max} = photosynthetic capacity) are model outputs. Steps colored green relate to whole-plant morphological and physiological traits. Modified from [40].

based on biochemical adjustments (e.g., Rubisco content), changes in leaf carbohydrate storage, leaf thickness, the number of mesophyll cells per unit leaf area and leaf nitrogen concentration (Fig. 5). The model predicts several acclimation responses (depending upon inputs), including up- and down-regulation of the net photosynthetic rate. The relative availability of carbon and nitrogen is centrally important to this model. When plants are grown in elevated $(pCO_2)_a$, carbohydrates become abundant relative to nitrogen. As a result the nitrogen concentration (n_m, g N g^{-1} leaf) decreases and leaf mass per unit area (h) increases. Ultimately the relative change in these two factors (n_m and h) can be used to predict photosynthetic responses. When elevated $(pCO_2)_a$ results in changes in h that are larger than the decreases in n_m, photosynthesis is predicted to be up-regulated, whereas when the decrease in n_m is larger than the increase in h, photosynthesis is predicted to be down-regulated. This model provides a framework for evaluating the existing data on plant response to elevated $(pCO_2)_a$, but leaves unanswered the question of what controls h and n_m.

CO_2 and the molecular biology of photosynthesis

The accumulation of non-structural carbohydrates is clearly important in the regulation of plant acclimation to elevated CO_2, if only for its effects on leaf thickness, specific mass (h) and nitrogen concentration. But it may also be directly involved in the mechanism responsible for photosynthetic acclimation. It has long been known that carbon metabolites are involved in the regulation of photosynthesis (reviewed in [41]), and the underlying molecular mechanisms of this control are now beginning to be understood. For example Sheen [42] has used chimeric genes to show that the transcription of seven different photosynthetic genes is repressed by glucose [42,43]. Suppression of non-photosynthetic genes by sugars has also been reported (reviewed in [41]), and it is now assumed that metabolic regulation of gene expression is a mechanism common to all higher plants. Glyceraldehyde, acetate and hexoses, including fructose, galactose and mannose, all have similar regulatory effects, although glucose may be the most important of these *in vivo* (J.R.S., unpublished data). The genes affected include those encoding carbonic anhydrase, D1 and D2 of photosystem II, cyt *f*, Rubisco small subunit and Rubisco activase ([44] and J.R.S., unpublished data).

A proposed model of the feedback effect of carbohydrates on Rubisco activity and content is diagrammed in Figure 6 (modified from [42,45]). Elevated CO_2 stimulates photosynthetic activity, as described above, and leads to the production of starch and triose phosphate in the chloroplast. Short-term regulation via Rubisco deactivation (reduced activity) can take place at this point if sucrose synthesis and/or export from the leaf is limited, decreasing P_i regeneration. The triose phosphates are transported

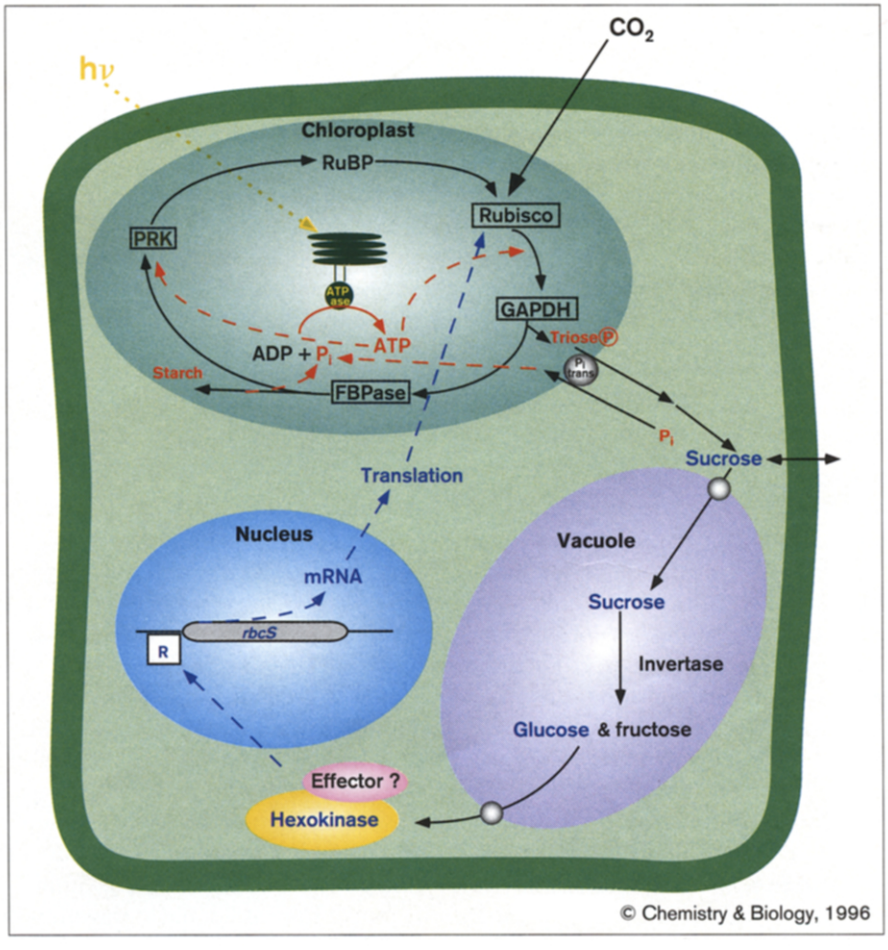
out of the chloroplast via a P_i transporter, and used to make sucrose in the cytosol. Once sucrose is present in excess, it is sequestered in a vacuole, where invertases can produce glucose and other active sugars that diffuse back to the cytosol. Subsequent phosphorylation of glucose by hexokinase is hypothesized to alter an as yet unknown effector molecule that ultimately leads to transcriptional repression in the nucleus. Glucose concentrations as low as 10 mM, well within a physiologically relevant range, can repress gene transcription [46–48]. Reduced gene transcription leads to reduced protein production, reduced photosynthetic capacity and ultimately reduced Calvin cycle activity and sugar production, completing the feedback mechanism. The Rubisco holoenzyme consists of eight small subunits (encoded by the nuclear *rbcS* gene family) and eight plastid-synthesized large subunits (from the chloroplast locus *rbcL*). The transcription of *rbcS* can be reduced in response to elevated $(pCO_2)_a$ [49], and decreased levels of *rbcL* mRNA in response to increased $(pCO_2)_a$ have also been reported, suggesting that both nuclear and chloroplast genes may be regulated by this proposed feedback mechanism [50].

CO_2 and whole plants

What determines the level of feedback regulation? Glucose and the other hexoses will only accumulate when increased photosynthetic carbon fixation is not matched by increased use. From the hundreds of published studies of the effects of $(pCO_2)_a$ on plant growth, it is generally concluded that C_3 plant growth and $(pCO_2)_a$ are positively correlated [6,51–53]. In agreement with this, both forest seedling growth and crop yield are stimulated by an average of ~32 % when plants are grown in a twice ambient pCO_2 as compared to ambient pCO_2 [6].

The controls on whole plant growth, carbon allocation and partitioning, plant development and phenology, and the interactions between these processes and photosynthesis

Figure 6



Model of cellular short- and long-term feedback regulation of photosynthesis resulting from elevated CO_2. Key regulatory enzymes (boxes) of the photosynthetic carbon reduction cycle (Calvin cycle) are shown in the scheme of the chloroplast; light energy ($h\nu$) supplies the ATP to reduce the C_3 products generated by Rubisco (see Fig. 3) into sugar phosphates (triose phosphates). An intermediate step catalyzed by glyceraldehyde 3-phosphate dehydrogenase (GAPDH) requires the consumption of NADPH (not shown), which is also produced in the light reactions. Fructose 1,6-bisphosphatase (FBPase) is a key regulatory enzyme; it catalyzes the conversion of fructose bisphosphate to fructose 6-phosphate + inorganic phosphate (P_i) as the Calvin cycle continues. The regeneration of RuBP is completed by phosphoribulokinase (PRK), which also consumes ATP. For the cycle to continue, the P_i consumed during the reduction processes (from ATP) must be replaced. Triose phosphates can be exported from the chloroplast envelope (P_i transporter) in exchange for P_i. When starch and sucrose synthesis is limited, however, P_i regeneration will slow and may limit ATP production and eventually the functioning of the Calvin cycle. This is known as short-term feedback regulation (red). Long-term feedback (blue) is probably realized through reduced gene transcription. Excess sucrose produced in the cytosol can enter the vacuole, where invertase can act upon it to produce hexoses. Glucose seems to be the primary active sugar for feedback regulation; it exits the vacuole, and is phosphorylated by hexokinase, initiating the feedback signal. Effectors may interact with hexokinase at this point to propagate a signal that enters the nucleus and acts as a repressor (R) of transcription of photosynthetic genes (e.g., a gene encoding the small subunit of Rubisco, *rbcS*). Rubisco levels may also be decreased by increased mRNA turnover, or by decreased translation. Modified from [41,45].

are not well understood. It has often been suggested that only plants primarily limited by carbon should respond to elevated $(pCO_2)_a$, but in most natural systems plant growth appears to be limited by other factors such as nutrient availability, water availability, or light. When plants are grown in limiting nitrogen concentrations, some experiments show a lack of a statistically significant CO_2 stimulation of growth whereas others show a constant relative increase in biomass regardless of nitrogen concentration (discussed in [6]). The overall level of increased world plant growth in response to the elevation in $(pCO_2)_a$ will ultimately be determined by a combination of carbon, nitrogen and water resources.

The interactions between carbon, nitrogen and water use can be complicated. For example, as well as directly stimulating photosynthesis, elevated $(pCO_2)_a$ usually leads to reduced stomatal conductance [54], in turn reducing transpirational water loss. Plants grown under water-stressed conditions or in arid regions may therefore be expected to benefit from increased water-use efficiency when $(pCO_2)_a$ is elevated. It has been predicted that a doubling of $(pCO_2)_a$ would result in a 50–70 % increase in net annual primary production (the net amount of carbon captured by plants) of desert ecosystems [55]. This increase in productivity is predicted to be greater than that for any other natural ecosystem, far exceeding the 0–20 % increase projected for the world's forest. Although this prediction is plausible, it is by no means certain. Increased water-use efficiency could lead to an initial expansion in leaf area, resulting in an increase in water loss that might balance or even surpass the savings realized through reduced stomatal conductance.

Many factors make the overall effect of increased $(pCO_2)_a$ difficult to predict. Stomatal closure can lead to increased leaf temperatures as a result of reduced cooling; increased leaf temperatures can alter the affinity of Rubisco for CO_2 and O_2, and can also alter the availability of the competing substrates, since the solubilities of CO_2 and O_2 are differentially affected by temperature. Carbon, nitrogen and water resources are often tightly linked, with the acquisition of one resource depending on the use of the others. The relationship between nitrogen availability and photosynthetic rate is particularly complex. Rubisco is the single most substantial nitrogen investment by the plant. If the plant reallocates its nitrogen resources away from Rubisco, this may paradoxically increase the photosynthetic rate by allowing an increase in the production of the enzymes that use triose phosphates (and an increase in the growth rate). This may reduce the production of sucrose, in turn reducing the production of the hexoses that down-regulate photosynthesis (see Fig. 6). Interactions between these resources can exist between and within all scales of biological organization, from molecular to ecosystem and even the biosphere.

Plants and the global carbon cycle

Development of a predictive understanding of ecosystem responses to global change depends on identifying the key processes that control the exchange of material, energy, and information on a variety of spatial and temporal scales. We need to understand photosynthetic carbon fixation via Rubisco and its implications at the scale of molecules, cells, organs, individuals, communities, ecosystems and the biosphere. Mooney [56] identified the lack of an integrated understanding of plant and ecosystem responses across spatial and temporal scales as one of the major factors limiting our ability to predict the response of ecosystems and the biosphere to changes in $(pCO_2)_a$. Understanding how carbon fluxes scale from the biochemical and molecular processes of photosynthesis to the system level is crucial, since ultimately one scale feeds back to the other. For example, if an increase in carbon fixation due to elevated CO_2 results in increased plant growth and stimulates net primary productivity by only 10 % globally, terrestrial plant carbon uptake would match present fossil fuel carbon emissions [6]. This stimulation of photosynthetic carbon uptake would at least temporarily limit further increases in $(pCO_2)_a$. Ultimately the majority of this carbon would not remain sequestered but would be released via autotrophic or heterotrophic respiration (Fig. 2). The 'residence time' or time delay in the subsequent release, through respiration, of the sequestered carbon is a critical variable affecting the global carbon cycle. For example, one model estimates that carbon stored in forested ecosystems may have an average residence time of nearly 30 years, whereas grasslands may store accumulated carbon for only 10 years (Y. Luo and J.F. Reynolds, unpublished data).

Recently it has been suggested that our understanding of photosynthetic sensitivity to CO_2 and long-term acclimation can be used to predict annual global carbon influx into terrestrial ecosystems due to photosynthesis. Luo and colleagues [57–59] have shown that the sensitivity of photosynthesis to $(pCO_2)_a$ is an invariant function across different C_3 species and environmental conditions. We can thus calculate an increase in carbon uptake as the product of the $\mathcal{L}$ function (the calculated sensitivity, based on a mathematical derivation of the model used to interpret $A:C_i$ curves (Fig. 4)) [60] and the current rate of carbon uptake. This model is an exciting advance and the $\mathcal{L}$ function has the potential to become an important scaling parameter for studying global terrestrial carbon cycling. It can be used to study the seasonal fluctuations in $(pCO_2)_a$ [61], global terrestrial carbon sequestration (Farquhar, G.D. and Lloyd, J., unpublished data, as cited in [57]), and carbon and nitrogen interactions in terrestrial ecosystems [57]. As the $\mathcal{L}$ function is based on the biochemistry of photosynthesis and the carboxylation of RuBP by Rubisco, this model reinforces the importance of photosynthesis as a major regulator of the global carbon cycle and the primary determinant of plant responses to $(pCO_2)_a$.

CO_2 inputs into the atmosphere via fossil fuel combustion and changes in land use are increasing the partial pressure of this trace gas at a rate not previously matched. Scientists with backgrounds in ecology, physiology, biochemistry and molecular biology are working together to understand the consequences of these changes. It is particularly exciting that progress in understanding an effect at one scale can be extrapolated to a variety of other scales. For example, progress in determining the molecular regulation of Rubisco and other photosynthetic proteins can readily be applied to photosynthetic biochemistry as interpreted from $A:C_i$ curves, and this information feeds directly into the modeling exercises predicting changes in global photosynthetic carbon flux.

Ultimately it is the implications of, and the interactions between, the primary responses of terrestrial plants to elevated $(pCO_2)_a$ that will determine the overall global response and constrain future biological regulation of the global carbon cycle. We have focused here on carbon inputs, but many more processes need to be considered. Respiration, transpiration, conductance, carbon and nitrogen allocation, competition, mineralization, decomposition, nutrient cycling and root exudation are among the other processes that can potentially be either directly or indirectly affected by elevated $(pCO_2)_a$. Human-caused release of CO_2 into the atmosphere is certain, but its results are not. Understanding the way that photosynthesis links biotic and abiotic carbon pools, and the effects of rising atmospheric CO_2 on this process, is critical if the human species is to be prepared for the 21st century and beyond.

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