Plant Physiology of the “Missing” Carbon Sink

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Plant physiology is deeply entwined with climate change. On one hand, many plant processes are climate sensitive. Plants are potential victims of climate change, threatened by novel conditions that stress natural ecosystems and tax the creativity of agronomists. On the other, plants are also major regulators of climate. One aspect of this regulation involves the absorption and dissipation of solar energy at the earth’s surface. A second involves the modulation of the water cycle through stomatal regulation of transpiration. In addition, plants influence climate through their role in the carbon cycle. Photosynthesis removes large amounts of CO_2 from the atmosphere. Global gross primary production or photosynthesis on land fixes about 20 times more carbon than is released by fossil fuel combustion (Table I). Respiration by plants and heterotrophs, plus biomass combustion, add it back. When photosynthesis outpaces respiration plus combustion, the land biosphere is a sink for carbon, reducing the rate of CO_2 accumulation in the atmosphere. When carbon losses outpace photosynthesis, the land is a carbon source.

Over the last 25 years, understanding the role of plants and ecosystems in regulating atmospheric CO_2 has been one of the central goals of global-change research. Although the understanding is not yet complete, the scientific framework is increasingly robust. It is unfortunate that the political framework for the use and abuse of the science is also well established.

Arrhenius (1) first predicted that industrial activity could lead to climate warming through increased absorption of thermal radiation by elevated atmospheric CO_2. Callendar’s (5) estimates of changes in atmospheric CO_2 from fossil fuel combustion, later confirmed by Keeling’s pioneering work with long-term monitoring (21), established the first component of the Arrhenius scenario. The last quarter century of intensive research with climate models, temperature records, and satellite observations has gone a long way toward establishing the second.

Early in the history of CO_2 research it was clear that only a fraction of the CO_2 emitted into the atmosphere from fossil fuel combustion was staying there. The other part was transferred to some kind of sink. Revelle and Seuss (25) and Bolin and Eriksson (4) calculated the expected transfer of CO_2 into the world’s oceans. Early syntheses of emissions, ocean uptake, and changes in atmospheric CO_2 suggested that the budget was close to balance and that the carbon in the land biosphere was stable or slightly increasing during the industrial era (2).

Another line of research indicated a critical problem with this approach. It was not accounting for CO_2 emissions from land use change, calculated by Woodwell and colleagues (30) to be in the same range as the emissions from fossil fuel combustion. If a large flux to the atmosphere was essentially invisible to the understood parts of the carbon cycle, it must be balanced by an unknown or “missing” sink.

Plant physiology provided a possible solution. In 1782 Senebier demonstrated that CO_2 is necessary for photosynthesis. Increases in the rate of photosynthesis with increasing CO_2 were documented around 1900 by Kreusler, Brown and Escombe, Treboux, and Pantanelli (23). With photosynthesis in C_3 plants increasing by 40% to 70% under a CO_2 doubling, it was reasonable to conjecture that the missing sink was somehow driven through CO_2 fertilization. Ecosystems on land were the most likely candidate locations because ocean photosynthesis is not simply related to the CO_2 concentration in the atmosphere.

Though attractive, this explanation for the missing sink had at least two important problems. First, the deforestation flux calculated by Woodwell and colleagues was probably too large to be balanced by CO_2 fertilization. Second, increased photosynthesis is not sufficient, by itself, to account for a large carbon sink. A large sink requires that the extra carbon fixed through photosynthesis must remain in the ecosystem for a substantial amount of time, on the order of decades.

Houghton and others resolved the first problem with improved estimates of CO_2 fluxes from land use change (11). Recent estimates of carbon emissions from land use and cover change are comparable, mostly in the range of 1 to 2 Pg year^{-1} (1 Pg = 10^{15} g), but with a large uncertainty (Table I). The magnitude of the sink from CO_2 fertilization is still not completely resolved. In the absence of a mechanistic formulation for the sink from CO_2 fertilization, Bacastow and Keeling (2) estimated the CO_2 fertilization effect as a residual. With estimates of the emissions from fossil fuel, plus uptake by the oceans, they assumed that the only missing term was the sink due to CO_2 fertilization on land. Knowing the historical trajectory of emissions and ocean uptake, it was

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Table I. *Summary of stocks and fluxes in the global carbon cycle*

All fluxes are Pg carbon per year. Stocks are Pg carbon. 1 Pg = 10^{15} g or 10^9 metric tons. The data are from references 26, 3, and 8.

CO_2 sources averaged over the 1990s	
Emissions from fossil fuel combustion and cement production	6.4 ± 0.5
Net emissions from tropical land use and land cover change	1.6 ± 1.0
Total anthropogenic emissions	8.0 ± 1.1
Carbon storage reservoirs averaged over the 1990s	
Atmospheric increase	3.2 ± 0.2
Ocean uptake	2.0 ± 0.8
Northern Hemisphere forest regrowth	0.5 ± 0.5
Other terrestrial sinks	2.3 ± 2.0
Fluxes in the "background" carbon cycle of the 1980s	
Land gross primary production	120
Land net primary production	56.4
Ocean net primary production	48.6
Stocks in the "background" carbon cycle of the 1980s	
Atmospheric carbon in CO_2	760
Land vegetation carbon	610
Soil carbon	1,580
Carbon in the ocean biosphere	3
Inorganic and organic carbon in ocean water	39,800

straightforward to calculate a CO_2 sensitivity of the historical missing sink. Looking for a simple, reasonable form, Bacastow and Keeling suggested that the extra CO_2 uptake changes with the natural logarithm of the ratio of current to pre-industrial CO_2.

Their expression is simple, but not mechanistic. It is based on plant physiology only to the extent that it suggests accelerating plant growth with increasing atmospheric CO_2. It has, however, been exceedingly important in efforts to understand options for managing the carbon cycle. The Intergovernmental Panel on Climate Change, the body asked by the world's governments to evaluate climate change and its impacts, stuck with this formulation for its major assessment reports in 1990 and 1995 (26).

By this time, however, the scientific understanding of CO_2 fertilization was becoming more multidimensional, with conflicting evidence from different approaches. It was also becoming more politicized. At the single leaf level, the model of Farquhar and colleagues (7) provided a reliable framework for evaluating the response of C_3 plants to elevated CO_2. With a combination of robustness and simplicity, this model has become almost a standard component in analyses of the global carbon cycle. At higher levels of organization, however, results were mixed. Some growth chamber experiments indicated dramatic increases in plant growth under elevated CO_2. These results rapidly became a rallying point for groups opposed to limits on CO_2 emissions. If elevated atmospheric CO_2 could lead to large increases in plant growth, it might produce a dramatic "greening of the earth" and plant uptake so large that it would eventually completely balance emissions from fossil fuel combustion. At least that was the argument in a famous 1991 video (14). Other studies, including work by Oechel, Strain, and Bazzaz, suggested much different responses, sometimes with relatively rapid decay of the initial growth stimulation and only small CO_2 responses in the long term (19).

By around 1990 it was clear that the basic questions about the CO_2 sensitivity of carbon storage could not be solved without moving to larger scales of space and time. The key issues concerned not the instantaneous response of photosynthesis to CO_2, but changes in photosynthetic capacity, biomass allocation, nutrient availability, and longevity of the plant and soil pools receiving the extra photosynthate. To address these issues many new studies have moved to the scale of entire ecosystems. Some emphasize vegetation near natural CO_2 springs (24). Others utilize a technology called FACE, or Free Air CO_2 Enrichment, in which an ecosystem is exposed to a computer-controlled cloud of elevated CO_2 (10).

These ecosystem-scale experiments document a number of artifacts associated with earlier CO_2 exposure techniques. For example, many examples of down-regulation of photosynthesis can be traced to limited rooting volume in pot experiments. On the other hand, the largest growth responses to elevated CO_2 occur in isolated plants, where an initial increase in growth produces a positive feedback through an increase in canopy size (20). Over many experiments, plant growth responses to approximately doubled CO_2 range from small decreases to increases greater than 100%, with mean increases around 50% for C_3 crops and 30% for woody plants (22).

The potential for this extra growth to drive carbon storage is still incompletely known. In some experiments, increases in respiration parallel increases in photosynthesis, minimizing the potential for storage (13). In others, carbon accumulates in biomass or soils (19). But even this is not a true index of long-term sink potential. Initial storage is almost unavoidable, as photosynthesis spurts ahead of respiration. The initial carbon storage in an experiment with an instantaneous CO_2 doubling is very difficult to relate to that ecosystem's potential for long-term storage (17). In fact, some of the negative feedbacks on storage, such as ecosystem-scale nutrient limitation, may develop only after several years of increased growth under elevated CO_2 (18). Of the global-scale models in wide use today, some postulate strong feedbacks from nutrient limitation, whereas others ignore the possibility completely (9). Long-term experiments are marching toward the evidence to reject one hypothesis or the other. Yet other long-term regulators of nutrient availability, from nitrogen fixation to exposure of soils with available phosphorus, are still very difficult to simulate with experiments or models. Progress on this front will require fundamental advances in understanding the factors that control whole-ecosystem nutrient budgets. These include retranslocation among plant tissues, the efficiency of foraging for nutrients, nutrient losses, controls nitrogen fixation, and the potential for limitation by nutrients other than nitrogen.

Experimental studies are providing increasingly refined estimates of net primary production or plant growth responses to CO_2 fertilization, and models are translating these into carbon sinks with increased sophistication. From the global end of the spatial scale, atmospheric methods are specifying the magnitude and location of the sinks. These methods work backwards from the spatial distribution of CO_2 concentrations in the atmosphere to infer spatial patterns of sources and sinks. This is essentially equivalent to using the entire atmosphere as a bunch of gas exchange chambers, with observed or modeled winds constituting the flows between them. Though this method is sensitive to a number of kinds of errors, the rich spatial and temporal patterns in atmospheric CO_2 suggest its potential (Fig. 1). Several atmospheric studies over the last decade indicate the existence of a large sink on land, especially in the middle to boreal latitudes of the northern Hemisphere (27). Similar studies augmented with information about ^{13}C in CO_2 and O_2, useful as probes to separate land from ocean sinks, confirm that much of the sink is on land and suggest that it has increased in the last decade (3). Eddy flux measurements, which quantify ecosystem CO_2 fluxes on a scale of 10^4 to 10^6 m^2, also confirm the existence of carbon sinks in an increasing number of temperate, boreal, and tropical forests (e.g. 29), though measurements in a few sites do not necessarily provide a regional perspective.

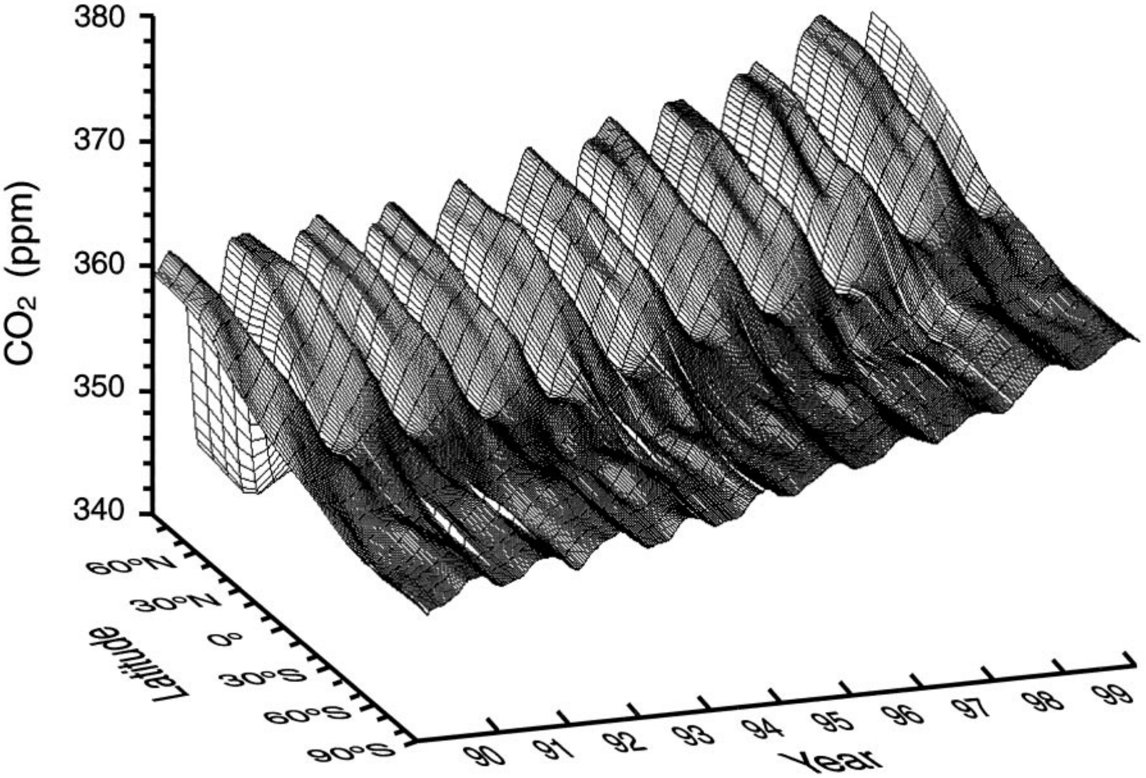

Figure 1. Temporal and spatial patterns in the concentration of atmospheric CO_2 showing the secular trend due to human emissions, the large seasonal fluctuations due to the terrestrial biosphere, and the spatial concentration differences that provide a basis for flux calculations with model inversions. Redrawn from reference 6, with updates from http://www.cmdl.noaa.gov/.

Atmospheric CO_2 is clearly rising. And there is definitely a CO_2 sink on land, probably averaging 2 to 3 Pg C year^{-1} during the 1990s, and as large as 4 Pg C year^{-1} in some years (3). Is CO_2 fertilization causing none, some, or all of the sink? This question can be approached from two perspectives. One is to simulate the CO_2 fertilization directly and to compare the estimate with the land sink. Using this approach, Kohlmaier and colleagues (16) estimated CO_2 fertilization to be about the magnitude required to explain the terrestrial sink. On the other hand, several more recent studies have concluded that the net primary production responses needed to generate the historical sink are too large to be consistent with CO_2 as the sole driver (28).

A second approach for estimating the role of CO_2 fertilization is to estimate the likely sinks due to other mechanisms and ask what is left for CO_2. Increasing evidence points to carbon sinks from a number of other mechanisms. In boreal and temperate latitudes, the regrowth of previously harvested forests appears to be important (15). Forest thickening due to fire suppression also appears to be a contributor. Agricultural practices that increase organic matter inputs to soil can also contribute to a sink (12). Because each of these processes is poorly known, it is not yet possible to employ them in precise estimates of the role of elevated CO_2 in the terrestrial sink. It looks likely, however, that CO_2 fertilization accounts for one-half of the sink or less.

Even if CO_2 fertilization is not the dominant driver of the terrestrial sink, it is still a substantial factor in the global carbon cycle. Future changes in CO_2 fertilization will significantly modulate the rate at which CO_2 increases in the atmosphere. Understanding that modulation and how it will change in coming decades will be a major contribution to a sustainable future.

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