PHOTOSYNTHESIS AND THE GREENHOUSE EFFECT

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The greenhouse effect, whereby atmospheric CO_2 and water vapour prevent the Earth's surface from being totally frozen is likely to be amplified by the anthropogenic emissions of fossil fuel CO_2. The global carbon cycle links photosynthesis to the greenhouse effect on all timescales up to millions of years. Major characteristics of the Earth's atmospheric composition, notably the low CO_2 and the high oxygen concentrations were created by the evolution of plant photosynthesis. The low CO_2 concentration in the atmosphere probably came about by the substantial acceleration of rock weathering that plants, especially angiosperms, cause. Calcium released by weathering moves to the oceans where it paces the formation of calcium carbonate rocks which are a massive carbon pool that dwarfs all others combined. On a timescale of 10^5 to 10^6 years the carbon from calcium carbonate is cycled back to the atmosphere via volcanoes.

On shorter timescales of sociopolitical concern photosynthesis is involved with the current global change in atmospheric CO_2 increase. From what we know about plant photosynthetic and growth responses to increasing CO_2 concentration interacting with other limiting environmental factors, it seems very likely that the biosphere is absorbing, into standing biomass and soil organic matter, some of the CO_2 emitted from fossil fuel burning and net deforestation thereby contributing to the "missing carbon" that does not appear as an increase in atmospheric CO_2 concentration. However, the scope for accelerating this CO_2 sequestering process by planting more trees is rather limited owing to the large scale required relative to the land available and to the fact that net carbon sequestration ceases when a forest matures.

INTRODUCTION

The interplay between photosynthesis and the greenhouse effect is so complex that there is no hope of presenting a complete and balanced picture in this brief contribution, if indeed a balanced picture is known to anyone yet. One of the reasons for complexity is that the controlling phenomena determining the inter-relationship are different over different timescales. The subject considered on the timescale of years is very different from the subject considered on the timescale of billions of years. Yet to really understand each timescale other timescales must be taken into account.

The global carbon cycle links photosynthesis and the greenhouse effect. To understand the global carbon cycle fully one needs to understand other biogeochemical cycles such as the hydrologic cycle, the nitrogen cycle, the oxygen cycle, the sulphur cycle, the silicate cycle, and the convection currents in the atmosphere, in the oceans, and in the Earth's mantle — the plate tectonic cycle. A biogeochemical cycle that appears to be in a steady dynamic equilibrium when viewed on a short timescale may well be far from equilibrium when viewed on a much longer timescale. For example, we might reasonably assume that over the early decades of the ninteenth century the global live plus dead organic matter pool in the biosphere was essentially in steady state over that timescale. However, over the 10,000 year post-glacial timescale, it was a net accumulator of carbon in soil organic matter especially in the tundra peats, where carbon may still be accumulating, be it slowly.

Further hampering the discussion, is the range of meanings of both the word "photosynthesis" and the phrase "greenhouse effect". To make sense of the interaction we need to define each.

The "*greenhouse effect*" now has four meanings depending on the context.

Arrhenius is reputed to have originally coined the term in the 1890s to represent the impact of the CO_2 content of the atmosphere, then about 290 ppm, on the vertical distribution of temperature in the atmosphere, the infra-red absorbing properties correctly being seen as keeping the lower atmosphere and ground warmer and the stratosphere cooler than would otherwise pertain. And since warmer conditions lead to a higher absolute moisture content of the atmosphere, there is a water vapour greenhouse effect that amplifies the CO_2 greenhouse effect, keeping the Earth's surface from being frozen-over completely. This I term the "*original greenhouse effect*".

Second there is the "*anthropogenic CO_2 greenhouse effect*" which refers to the predicted further warming of the global surface temperature associated with the presumably man-caused increase in atmospheric CO_2 concentration since industrialization started last century. This arises not because the increase in the atmospheric content of causes increased total absorption of infra-red back radiation, but because it has the effect of concentrating such absorption into a lower portion of the atmospheric depth thereby cooling the upper portion.

Third, there is the "*augmented anthropogenic greenhouse effect*", in which the observed increase in other radiatively active atmospheric constituents like methane, chloro-fluorocarbons, nitrous oxide, and ozone are adding to the effect of increasing CO_2 concentration, because they absorb at different wavelengths than do CO_2 and H_2O vapour.

And finally, there is the "*journalists' greenhouse effect*" in which a range of phenomena more or less, or possibly, related, including the augmented anthropogenic greenhouse effect, the CO_2 fertilizing effect, the stratospheric ozone-hole over Antarctica, UV radiation at ground level, sea level change, recent warm winters and droughts in some places, and deforestation of the Amazon Basin, are all *embraced by the one phrase — the greenhouse effect* — now often truncated to just "*greenhouse*".

Photosynthesis comes into many aspects of the phenomena embraced by these different elements of the greenhouse effect.

PHOTOSYNTHESIS

At the lowest level of organizataion plant photosynthesis is a membrane-bound process in which the energy of light photons is harnessed to separate change across a membrane leading to oxidation of a reductant in abundant supply in the environment and the formation of chemical energy and reducing equivalents that are subsequently available for synthesis of organic molecules.

While, to the photosynthetic purist, such consequential synthesis may not in itself be photosynthesis, to most biologists it is acceptable to include the formation of at least the first stable product as part of the process. To whole-plant physiologists, steps subsequent to formation of the first stable organic molecule, such as sucrose and starch production, are also usefully included as part of a multi-step process of "*photosynthesis*".

For higher plants the abundant environmental reductant is water, the first stable products are ATP and NADPH, and the product to the environment is oxygen.

There is now little doubt that the world's atmosphere was virtually anaerobic until the evolution of a form of photosynthesis able to utilize water as reductant came into existence (Walker, 1984). Oxygenic photosynthesis blossomed 2 or 3 billion years ago and has raised atmospheric oxygen from virtually zero to the present 0.2 atmospheres. This has had profound effects on other geochemical cycles such as the carbon cycle and hence on global climate via the original greenhouse effect. Also since it is the interaction of UV-radiation with O_2 that produces the UV screening stratospheric ozone layer, oxygenic photosynthesis led to the low level of UV that now occurs at ground level. This permitted higher forms of life to develop.

When one stands back from the photosynthetic membrane to view the green leaf mesophyll cell as the minimal unit of photosynthesis, then the inputs become light, water, and carbon dioxide and the outputs are sucrose and oxygen. But embedded inside is an O_2/CO_2 cycle involving the interplay between photosynthesis and photorespiration. Photorespiration is a process, involving 3 subcellular organelles working together, to retrieve carbon that would otherwise be lost to atmosphere. But in the process some recently fixed CO_2 is nevertheless lost to atmosphere.

Figure 1 (from Gifford, 1988) shows how the central enzyme of the CO_2 fixation cycle — ribulose bisphosphate carboxylase or RUBISCO — also reacts with O_2. It is believed that the reaction with O_2 is inevitable and that much of photosynthetic evolution has focussed on minimizing the rate of this reaction. When O_2 reacts with ribulose bisphosphate, phosphoglycollate is produced. The photorespiration cycle serves to recover half of the carbon of phosphoglycollate at the expense of losing half of its carbon as photorespiratory CO_2. So the presence of O_2 reduces CO_2 fixation rates by three mechanisms: (1) by competitive inhibition of carboxylation, (2) by consuming some of the ATP made by the photosynthetic light reactions, and (3) by releasing some of the recently fixed CO_2 back to atmosphere.

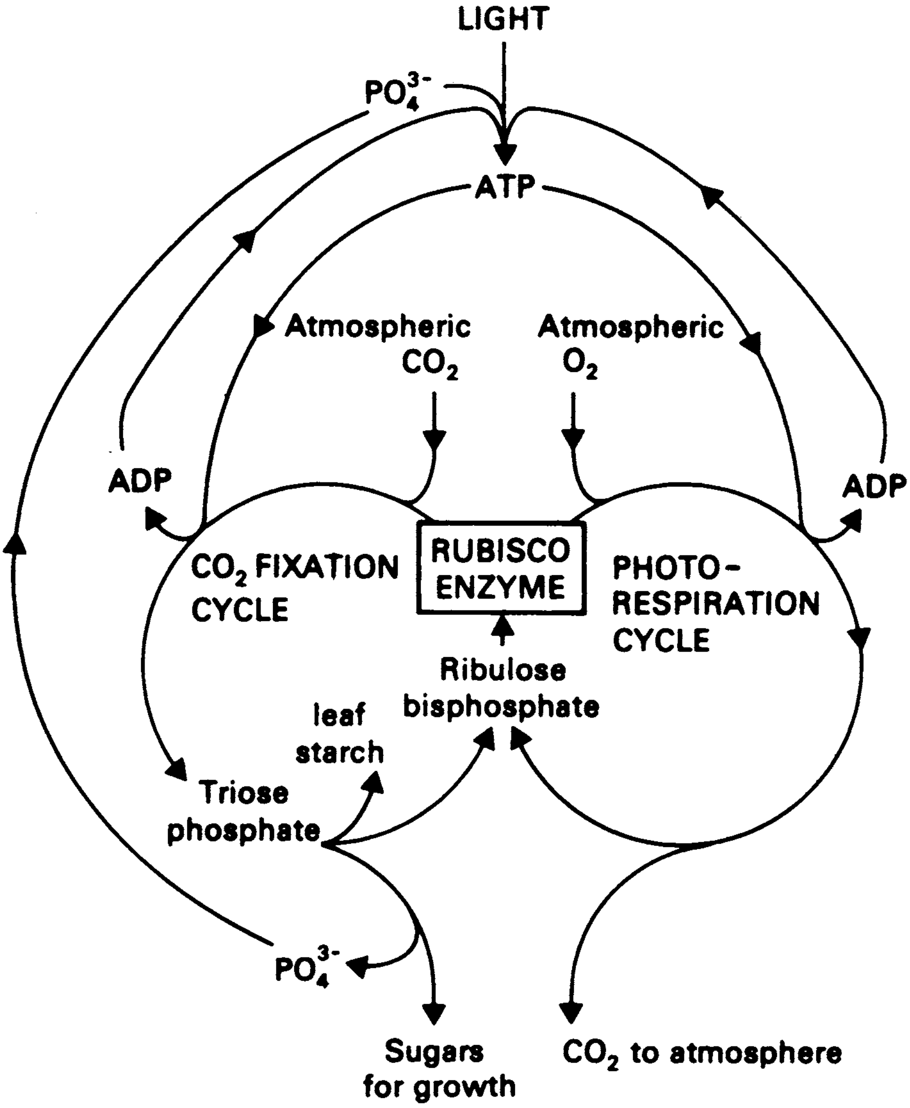


Fig. 1. Essential features of the interplay between the photosynthetic CO_2 fixation cycle and the photorespiration cycle of the mesophyll cell of C_3-species' leaves (Gifford, 1988a).

Although this internal cell cycle may appear to be inconsequential to the big picture of the global carbon cycle and the greenhouse effect, I believe that in fact it may be of considerable consequence in attenuating the current anthropogenic build up of atmospheric CO_2 in the short term.

Skipping over the individual leaf as a photosynthetic unit we can move on to the whole plant during growth. Taking the system boundary as the epidermis of the plant, and the time-frame as 24 hours, the inputs are CO_2, light and water, and the outputs are the daily increment of plant dry matter and O_2. However, the input CO_2 is net of CO_2 that is released by true (dark) respiration as well as by photorespiration.

At an ecosystem level over a whole annual cycle, the metabolism of animals and soil microorganisms is now a functional part of the photosynthesising ecosystem, and the input CO_2 is net of the CO_2 emitted by heterotrophic organisms such as decomposers. The system could not function for long without them. When annual decomposition matches annual accrual of live and dead dry matter, the net annual photosynthesis rate of the system as a whole is zero. This is what happens to a mature ecosystem integrated over a wide area. However, although one might think, as a result, that such a mature ecosystem is neutral in the dynamics of the global carbon cycle, this is *not* the case in the long term. The photosynthesis of such a system is critically involved in the biggest carbon cycle of them all — *the carbonate-silicate cycle* that determines the global atmospheric CO_2 concentration, and hence world climate, on the geological time scale of millions of years.

GLOBAL CARBON POOLS FLUXES, AND CYCLES

Some major rates and magnitudes of carbon flows and pools in the global C-cycle are helpful in understanding the carbonate-silicate cycle.

The quantity of carbon in circulation in the global carbon cycle is vast compared with the amount in the atmosphere at any one time (Table 1). The data in this table

TABLE 1: Some Global Carbon Pools Relative to the Atmospheric Pool Set at Unity (From Gifford, 1988)

Present atmosphere	1.0
Present biosphere:	
living on land	0.9
dead on land	2.8
live at sea	< 0.01
dead at sea	1.8
Dissolved in the ocean:	
surface mixed layer	1
thermocline	12
deep ocean	50
Sedimentary rocks:	
on land in reduced form	17,000
on land in oxidised form	43,000
under the sea, reduced	10,000
under the sea, oxidised	24,000

are presented relative to the amount of carbon in the present-day atmosphere. The rapidly exchanging pools of the atmosphere, the standing ('live') biomass and the well-mixed surface oceans are all of similar size [approx. 600Gt(C)]. These fast turnover pools contribute carbon to the much larger, slow turnover pools. Given that all these pools are exchanging carbon with one another, one can see that *given long enough* man-induced transfers of carbon from the reduced rock carbon (coal) to the atmosphere are likely ultimately to be re-distributed to the other pools. In the meantime we have to live with the transient perturbations that we are creating—but this transient may outlive civilization and *Homo sapiens.*

The key rates of exchange between some of these pools are indicated in Table 2. Relative to the annual increase in atmospheric CO_2 concentration, annual C turnover between net primary production (NPP) by photosynthesis on land and its decomposition back to CO_2 is large. In fact, the uncertainty in our estimate of global net primary production and of decomposition, is greater than the observed annual increase in atmospheric CO_2 of 3 Mt (carbon). So although no-one expresses any doubts that the 5.6 Gt yr^{1} of fossil fuel CO_2 release is the cause of the approximately 3 Gt yr^{1} of atmospheric CO_2 increase, it is not possible yet to state unequivocally how much of the other 2.6 Gt p.a. is sequestered into the terrestrial biosphere despite net deforestation of 0.4 to 2.4 gigaton per annum (Houghton and Woodwell, 1989).

The other possible sink is the oceans, and marine photosynthesis would play a role there. In the short term, marine photosynthesis can pump CO_2 down into deeper waters via decomposition of dead marine organisms to CO_2, as they precipitate out through the thermocline and deep ocean redissolving as they fall. Some of the dead organisms with their carbonate shells do reach the ocean floor where they ultimately form carbonaceous rocks that become subducted by plate tectonic movements into the molten magma. Reaction with molten silica causes release of

TABLE 2: Some Global Carbon Flows Between Pools in Gt(Carbon) Per Annum

1980s rate of increase in atmosphere	3
Geosphere to atmosphere transfer:	
from fossil fuel burning	5.6
natural	0.1
Atmosphere to land biosphere transfer (net primary production)	about 60
Land biosphere to atmosphere (decomposition)	about 60
Net atmosphere to land biosphere (sequestration)	0 - 3
Net land biosphere to atmosphere (deforestation)	0.4 - 2.4
Atmosphere to ocean	about 90
Ocean to atmosphere	about 90
Ocean to geosphere transfer	0.1

carbon dioxide which re-enters the atmosphere and oceans by magmatic outgassing (volcanoes, etc.), thereby completing the slowest turning carbon cycle, *the carbonate-silicate cycle*. This cycle has a carbon turnover time of about a million years.

Over that long timescale, it is the balance between carbon deposition in solid form on the ocean floor and CO_2 outgassing from the mantle into the atmosphere that determines the CO_2 concentration in the atmosphere. The smaller biological and oceanic C-cycles are of little consequence on that timescale. But surprising as it may seem, photosynthesis probably plays a critical role in the balance of this carbonate-silicate cycle and hence in long term atmospheric CO_2 concentration. This is because terrestrial photosynthesis probably sets the pace of solid carbon compound deposition on the ocean floor. It works as follows.

PHOTOSYNTHESIS AND THE CARBONATE/SILICATE CYCLE

The removal of carbon into ocean sediments is partly as dead organic matter but mostly as calcium carbonate. The organic sediments are obviously the product of photosynthesis. It is not yet settled as to the extent of biological formation of calcium carbonate shells, as distinct from its physico-chemical precipitation, in ocean floor deposition of carbonate (Wilkinson and Walker, 1989), but certainly biological shell formation is very important for accelerating carbonate precipitation and may predominate. However, whether it is biological or physico-chemical, solid carbonate cannot be formed without an input of Ca^{++} or Mg^{++} ions. Continued formation of solid carbonates therefore depends on renewal of Ca^{++} and Mg^{++} ions in the ocean which arrive via the rivers along with bicarbonate ions. These ions reach the rivers by weathering of calcium and magnesium silicate rocks and carbonate rocks on land. So the formation of marine carbonates, that remove CO_2 from the atmosphere, is paced by the rate of weathering of the rocks on land (Berner and Lasaga, 1989).

The rate of rock weathering is determined in turn by the exposed surface area of rock, the CO_2 concentration at the rock surface, other acids at the rock surface, rainfall and run off, and temperature. The reaction with CO_2 is:

$$2CO_2 + H_2O + CaSiO_3 = Ca^{++} + 2HCO_3^- + SiO_2$$

The three moieties produced, run off in the drainage water ultimately out to sea.

Photosynthesis on land sets the pace for this weathering process, enhancing it considerably over that which would otherwise pertain (Knoll and James, 1987). It can do this by several mechanisms. Photosynthesis drives the growth of plants which send roots down in search of water and mineral nutrients. Roots and associated micro-organisms accelerate the break-up rock in the process of soil formation thereby enormously increasing the surface area of rock. Roots also give off CO_2 by respiration and exude organic acids. Furthermore, microbial decomposition of dead roots also increases the CO_2 concentration in the soil where it may be one or two orders of magnitude more concentrated than in the open atmosphere.

In these ways the rate of rock weathering is greatly accelerated by the photosynthesis-decomposition cycle. The mineral ions are taken up into the plant and eventually leached from the nutrient cycle of the ecosystem and washed into the ocean.

So now we can come back to the definition of photosynthesis, this time on the scale of the terrestrial biosphere. On that scale, photosynthesis is a process the inputs to which are light, CO_2 and unweathered rock, and the outputs of which are mineral ions, especially calcium and magnesium, bicarbonate and silica into the ocean. Most of the carbon involved is just a component that is cycled between atmosphere, live plant, dead organic matter and microbes, catalysing the transfer of mineral ions from land to sea. The hydrologic cycle also helps it along.

So by this mechanism terrestrial photosynthesis paces the removal of atmospheric CO_2 into the deep ocean sediments and hence into the tectonic subduction zones. By pushing the balance between magmatic and volcanic outgassing of CO_2 and tectonic removal of CO_2 in favour of removal, terrestrial photosynthesis holds atmospheric CO_2 at a much lower value than would otherwise be.

This in turn has reduced the magnitude of the "original greenhouse effect" warming. Walker, Hays and Kasting (1981) have proposed that there is an element of negative feedback regulation over the greenhouse effect on geological timescales because weathering rate is positively temperature dependent. Introduction of vegetation photosynthesis and decomposition into the consideration, further strengthens this negative feedback, considering both the strong positive temperature dependence of primary productivity and its positive CO_2 dependence (see below).

Consider for example the implication of the increase of solar luminosity by 30% during the history of the Earth (Lovelock and Whitfield, 1982). Increasing luminosity increases surface temperature which increases rock weathering rate. It also increases both photosynthetic productivity and soil organic matter decomposition rate which would increase root-zone biological activity and hence rock weathering. Since the rate of rock weathering paces (via ocean biological productivity) the rate of carbonate deposition, atmospheric CO_2 declines leading to cooling that offsets the initial warming owing to increased luminosity. It is proposed that the progressive decrease of atmosphere CO_2 by that mechanism over Earth history, and concurrent overall cooling has occurred by this interplay of photosynthesis and the greenhouse effect, despite the continuous increase in solar intensity.

Further developing this concept of profound photosynthetic involvement in atmosphere CO_2 control over geological timescales via the carbonate-silicate cycle, Volk (1989) has proposed that the substantial displacement of gymnosperms by angiosperms 60-70 million years ago, caused a decrease in atmospheric CO_2 and a consequential reduction in global temperature of several °C. This is because angiosperms, with their deciduous photosynthetic habit, cause Ca^{++} and Mg^{++} loss to the oceans to be 3 to 4 times faster than do evergreen gymnosperms (Knoll and James, 1987).

So it is because of the evolution of photosynthesis and particularly of the deciduous habit of most angiosperm trees that global CO_2 concentration had declined to a level about as low as it can get (Lovelock and Whitfield, 1982). That is, before industralized man started cutting down the trees and burning fossil fuels, when it started to go up again around the middle of the nineteenth century A.D.

SOCIOPOLITICAL CONCERNS

This brings us back to the anthropogenic CO_2 greenhouse effect and the involvement of photosynthesis on much shorter timescales of decades (rather than millions of years)—the scale of sociopolitical significance today. Two issues of current concern are:

1. Does the photosynthetic response to CO_2 concentration observed in laboratories have any implication for understanding where anthropogenically emitted CO_2 goes?
2. Can a tree planting policy have much relevance to ameliorating atmospheric CO_2 build-up owing to fossil fuel burning?

That leaf or plant photosynthesis is CO_2-dependent in the short term has been demonstrated frequently. It is illustrated here (Fig. 2) at the whole plant level for the gymnosperm *Pinus radiata*, measured at one third full sunlight intensity of 600 µmol (photons) m^{-2} s^{-1}. This is a light intensity at which rate of photosynthesis is limited by light. In fact whole-plant photosynthesis was almost linearly dependent on light at that level. So given the concept of the law of limiting factors how can it be that photosynthesis is both light-limited and CO_2-limited concurrently?

The answer lies in *photorespiration*. As mentioned, photorespiration occurs because the active centre of the carboxylating enzyme RUBISCO also reacts with O_2 leading to a series of biochemical reactions leading to some loss of CO_2. Thus O_2 is a competitive inhibitor of carboxylation. And that is so, no matter what the level of ribulose bisphosphate (RuBP). RuBP concentration is determined by the light intensity. So even at low light intensity, higher CO_2 concentration will compete with O_2 and thereby reduce photorespiratory losses from the plant. Thus ecosystems that are light-limited such as humid tropical rainforest, or cool temperate forests also have had the opportunity to photosynthesise faster as CO_2 increased.

Elsewhere water is growth-limiting. Not only does high CO_2 increase photosynthesis it also reduces the aperture of stomata—the small pores in the surface of the leaf. This has the potential to reduce transpiration. Since water loss is the price that plants pay for opening their stomata to let CO_2 in for photosynthesis, an increase in CO_2 concentration increases the WUE of plant growth as illustrated in Figure 3 for wheat. Note the more restricted the water supply, the greater was the CO_2 effect on water use efficiency.

Another factor limiting the growth of plants is the nitrogen supply. Again, it has been observed that high CO_2 concentration increases the efficiency with which this growth-limiting nutrient is used by plants. Furthermore, at high CO_2, nitrogen

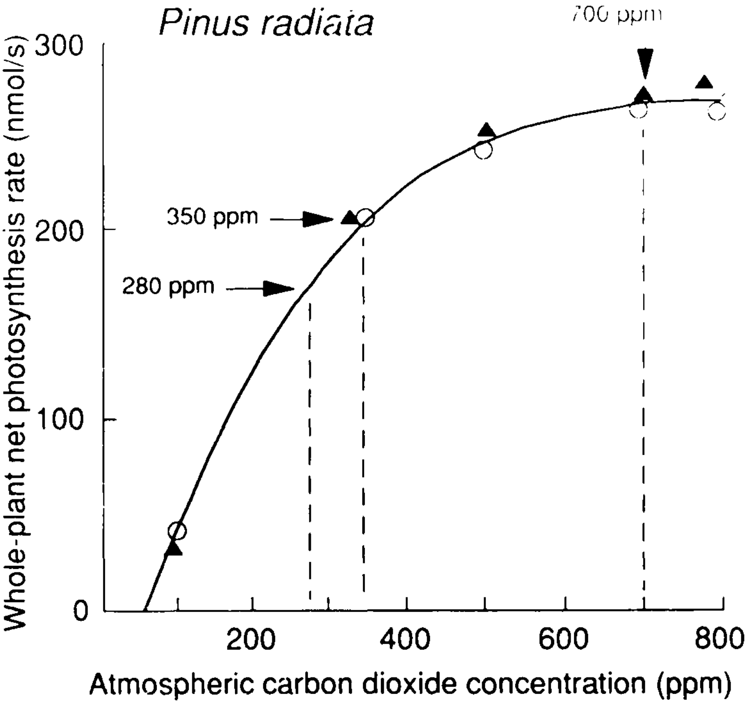


Fig. 2. Response of whole-plant photosynthesis (corrected for dark respiration) of a *Pinus radiata* (Monterey Pine) sapling, to atmospheric CO_2 concentration. Photosynthetic photon flux density was 600 μmol(photon) m^{-2} s^{-1} (Gifford, unpublished).

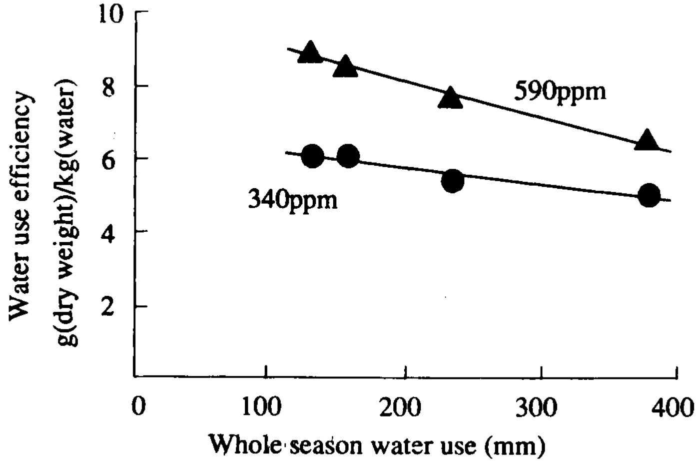
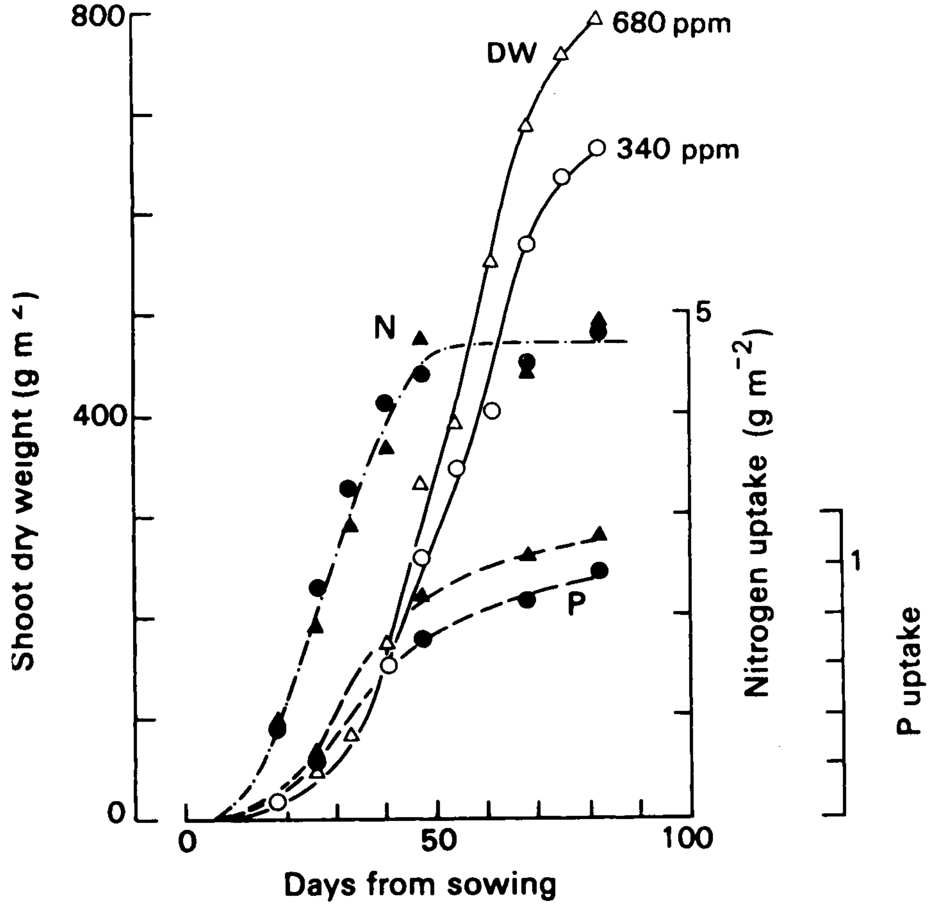


Fig. 3. Water use efficiency of water-limited seasonal wheat growth at two levels of atmospheric CO_2 concentration (Gifford, 1979).



ig. 4. Time-course of shoot growth of wheat grown with nitrogen limitation at two levels of atmospheric CO_2 concentration. The nitrogen limitation is indicated by the failure of the CO_2 enriched crop to take any more nitrogen from the soil (▲) than the control crop (●). (Gifford and Morison, unpublished).

xing legumes fix more nitrogen. The example in Fig. 4 is for wheat canopies grown ith fixed and limiting nitrogen supply. They were able to accrue more dry weight espite the low amount of N available.

Similarly, what scarce evidence there is seems to indicate that even phosphate mited plants can grow faster at high CO_2. However, the evidence is more equivocal that interaction (Conroy and Barlow, 1987).

So, the prediction based on such results from studies in controlled environments, that vegetation in the field is likely to be growing faster as CO_2 concentration creases. This has to be tested somehow in the field, but that will be a massive task–

especially for forests. Also there is the question of whether any CO_2 stimulated incremental growth is being distributed into slow turnover pools of the ecosystem like tree trunks and soil organic matter. But there is little evidence on that.

I made a "guesstimate" of the possible magnitude of the sequestering of carbon in slow turnover pools of the global biosphere, on account of the CO_2 concentration increase since systematic monitoring began in 1958 (Gifford, 1980). I arrived at the conclusion that 1-2 Gt(C) yr^{-1} could have then been being removed from the atmosphere by that mechanism alone. When one considers the further increase in atmospheric CO_2 before and since that period together with the huge amounts of oxidised N, S and P that we are artificially putting into the global environment, it seems very likely indeed that the biosphere is sequestering something like 1-2 Gt(C) yr^{-1} extra each year (Gifford, 1988b).

POTENTIAL FOR REFORESTATION

On the question of whether we can use re-afforestation to slow down the rate of CO_2 increase, the opportunity seems to be minimal (Gifford, 1988a, 1989). Marland (1988) suggested that it would take an area of about 700×10^6 ha of fast-growing forest to absorb the annual global CO_2 emissions from fossil fuel burning. This is an area the size of Australia. Australia produces fossil fuels with a carbon content of 150 million tons yr^{-1}. About half of this is exported.

Plantation forests, on the best sites in Australia, accrue carbon into stemwood during their 30-60 year growth period at about 5t(C) ha^{-1} yr^{-1} on average. Thus to mop up 150Mt(C) yr^{-1} into stemwood Australia would need a new forest of 30 million hectares actively growing on sites which did not already bear forest i.e. on arable and pasture land (Gifford, 1989). When one considers that the area of arable and improved pasture in Australia is only 48 million hectares, and the area of remaining forest is 41 million hectares, only 1 million of which was planted, one can see what a small contribution planting special trees for mopping up atmospheric CO_2 can make on that continent given alternative land use constraints.

Furthermore, once planted such a forest must stay in place in perpetuity if the objective is to permanently keep a pool of carbon, as live and dead organic matter, out of the atmosphere. Scenarios in which, at maturity, the forest is felled for conversion to wood-products of various longevities before decomposition or burning, do provide some scope for carbon sequestration but less than if the mature forests were left undisturbed (Barson and Gifford, 1990).

SUMMARY

Photosynthesis, then, plays a critical role in many aspects of the global carbon cycle and hence in world climate and the greenhouse effect. But we cannot regard it as providing a panacea for public policy to get us out of "greenhouse" trouble over the timescale of years to decades.

REFERENCES

Barlow, E.W.R. and Conroy, J. (1988). The influence of elevated atmospheric carbon dioxide on the productivity of Australian forestry plantations. in Greenhouse: Planning for Climate Change. G.I. Pearman (Ed). Leiden, E.J. Brill, pp. 526-533.

Barson, M. and Gifford, R.M. (1990). Carbon dioxide sinks: The potential role of tree planting in Australia. in Greenhouse and Energy, Proceedings of a conference held at Macquarie University, Dec 3-8, 1989. Submitted.

Berner, R.A. and Lasaga, A.C. (1989). Modelling the geochemical carbon cycle. *Scientific American*, **260**, 54-61.

Gifford, R.M. (1979). Growth and yield of CO_2-enriched wheat under water limited conditions, *Aust. J. Plant Physiol.*, **6**, 367-378.

Gifford, R.M. (1980). Carbon storage by the biosphere. in Carbon Dioxide and Climate: Australian Research. G.I. Pearman (Ed). Canberra. Australian Academy of Science, pp. 167-182.

Gifford, R.M. (1988a). Direct effects of higher carbon dioxide concentrations on vegetation. in Greenhouse: Planning for Climate Change. G.I. Pearman (Ed). Leiden, E.J. Brill, pp. 506-519.

Gifford, R.M. (1988b). Global photosynthesis, atmospheric carbon dioxide and man's requirements. in Current Perspectives in Environmental Biogeochemistry. G. Giovanozzi-Sermanni and P. Nannipieri (Eds). Rome. C.N.R.-I.P.R.A, pp. 413-444.

Gifford, R.M. (1989). Trees in the global greenhouse—Their role and potential. *Trees and Natural Resources*, **31** (1), 9-11.

Houghton, R.A. and Woodwell, G. (1989). Global climate change, *Scientific American*, **260**, 18-27.

Knoll, M.A. and James, W.C. (1987). Effect of the advent and diversification of vascular land plants on mineral weathering through geologic time, *Geology*, **15**, 1099-1102.

Lovelock, J.E. and Whitfield, M. (1982). Life span of the biosphere, *Nature*, **296**, 561-563.

Marland, G. (1988). The prospect of solving the CO_2 problem through global reforestation. Washington D.C., United States Department of Energy. TR039 (DOE/NBB-0082). 66p.

Volk, T. (1989). Rise of angiosperms as a factor in long-term climatic cooling, *Geology*, **17**, 102-110.

Walker, J.C.G. (1984). How life affects the atmosphere, *Bioscience*, **34**, 486-491.

Walker, J.C.G., Hays, P.B. and Kasting, J.F. (1981). A negative feedback mechanism for the long-term stabilization of Earth's surface temperature, *J. Geophys. Res.*, **86**, 9776-9782.

Wilkinson, B.H. and Walker, J.C.G. (1989). Phanerozoic cycling of sedimentary carbonate, *Amer. J. Sci.*, **298**, 525-548.