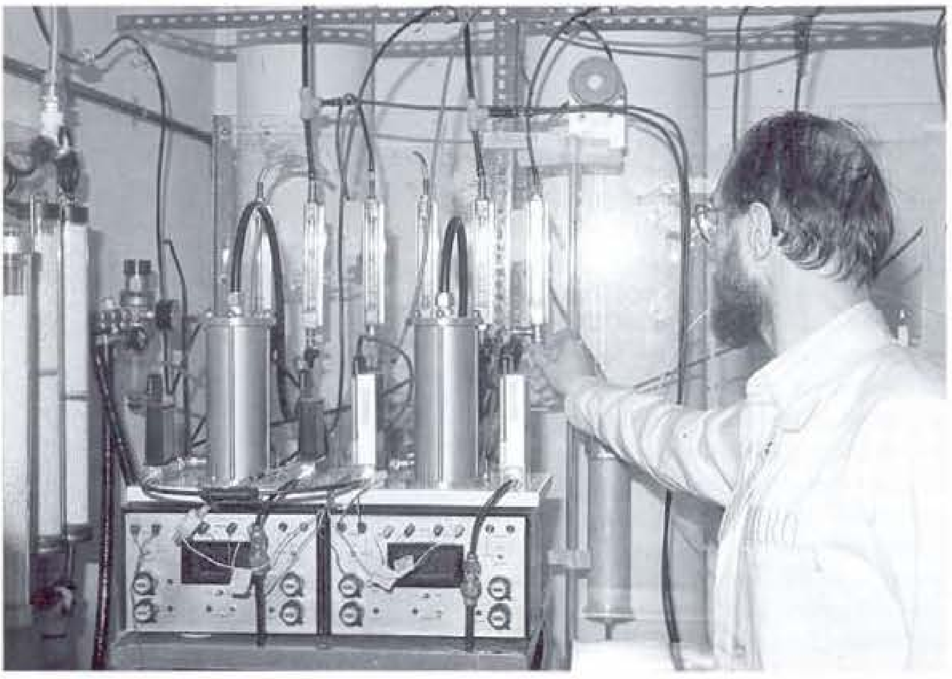
The greenhouse effect — not all bad?

We hear a lot these days about the 'greenhouse effect' — the likely changes in the weather caused by the atmospheric build-up of gases, especially carbon dioxide, as a result of human activity. However, we don't know much about the 'plant-fertilising effect', a possible silver lining inside that climate-changing greenhouse cloud.



Dr Gifford with his CO_2-generators. All CO_2 from the outside air is removed, and then the gas is added back to give the desired concentrations. This procedure avoids the slight fluctuations in atmospheric CO_2 that normally occur.

Carbon dioxide is essential for plant growth, and yet only exists in the air in vanishingly small amounts. Much of the anatomy, physiology, and biochemistry of plants is tailored to achieving the difficult goal of extracting this trace gas, used as a raw material for photosynthesis — the process whereby plants make their own food in the form of sugar. This they then distribute to all their cells for use as a fuel. The glucose in our blood acts in the same way.

As plant cells respire the sugar in the course of their normal metabolic reactions they produce carbon dioxide (CO_2) as waste. This respiration is continuous but, under the right conditions, the photosynthesis during the day takes more carbon from the air than respiration releases, and the plant ends up with a net carbon surplus that enables it to grow.

The energy in light powers photosynthesis, although the process also needs water and various other factors (see the box for more detail about this amazing piece of chemical wizardry). But a substance that's often in short supply — a limiting factor of photosynthesis — is carbon dioxide.

For a number of years, Dr Roger Gifford of CSIRO's Division of Plant Industry in Canberra has been studying the effect on plant growth of increasing the carbon dioxide concentration, with a view to assessing the repercussions that the CO_2 build-up may have on the world's vegetation.

His work indicates that the biosphere could possibly be helping to soak up some of the extra CO_2 that human activity releases, although it may not be able to do it as quickly as we would like. That atmospheric CO_2 is steadily rising is indisputable, so we are producing CO_2 faster than the plants and other 'sinks' can take it up. To be strictly accurate: the world's vegetation annually traps at least ten times more CO_2 than our fossil-fuel burning releases. However, plant respiration and decomposition in the biosphere release most of this back again, so we are therefore talking about the net — not absolute — ability of vegetation to store carbon compounds derived from CO_2.

Calculations show that the amount of CO_2 we are releasing is about twice as much as that accounted for by the measured increase in its atmospheric concentration. The remainder disappears into various known 'sinks' — the largest being sea water, into which the gas dissolves. But some is still unaccounted for, and it appears likely that this small amount of 'slack' is being taken up by the more vigorous growth of plants — in the sea as well as on land.

In general, plants do indeed benefit from increased levels of CO_2.

We should certainly not be sceptical about plants having the ability to modify the earth's atmosphere. After all, they profoundly influenced it in the past. Aeons ago, carbon dioxide was far more abundant in the atmosphere than today, and oxygen was probably absent. As CO_2 escaped from the inner earth, simple plants steadily took up most of it by photosynthesis, turning it into organic molecules — the majority of which sedimented into rocks, although a small proportion eventually became the vast subterranean deposits of coal and oil that we burn today. At the same time, oxygen — the waste product of this type of photosynthesis — was released into the atmosphere and the animals that evolved took advantage of it.

The higher plants of today are adapted to the scarce levels of photosynthesis's chief raw material, and to the fact that oxygen can interfere in the process. (The plant enzyme that 'fixes' atmospheric carbon dioxide into an organic molecule is rendered less efficient by the presence of oxygen, which competes with CO_2 for attachment to the enzyme — but more of this, and its consequences, later.)

CO_2 abundance

So what results do increases in the concentration of CO_2 have on organisms that are adapted, in effect, to 'scraping' a living

How plants make food

Why not use solar energy to make food from just water and a waste gas? If only we could! But green plants manage it every day by means of photosynthesis.

The process is immensely complex and has intrigued biochemists for decades. Thanks to much hard work by a number of people, we now understand the procedure in outline, although we are far from being able to duplicate it.

Photosynthesis has two parts: one is the chemistry of carbon dioxide fixation; the other involves capturing photons of light and providing energy and hydrogen for the chemical reactions.

Let's start with the chemistry: the enzyme ribulose bisphosphate carboxylase ('rubisco') attaches CO_2 to an organic compound (naturally, ribulose bisphosphate), containing five carbon atoms. Rubisco is large and rather slow — catalysing only a few reactions per second instead of at least a thousand like an 'average' enzyme — so, in order to get enough CO_2, plants need a lot of it; indeed, it may account for about 50% of the soluble protein in green plant cells, and is probably the most abundant protein in the world.

Following its combination with CO_2, a cycle of chemical transformations occurs that regenerates the starting substance ribulose bisphosphate. For every three CO_2 molecules that enter the cycle, three starting molecules are produced, along with one molecule called glyceraldehyde. The last-named consists of three carbon atoms, three oxygens, and five hydrogens, and is a simple carbohydrate. The plant cell can readily transform this central molecule into various types of sugar, and thence starch, or can put it to good use in the manufacture of other important compounds.

In essence, the carbon fixation cycle condenses three carbon dioxide molecules and adds hydrogen atoms. To do all of this takes energy, which arrives at the enzymes in a biochemical form, but which ultimately comes from light. The light-requiring reactions split molecules of water — precisely how is still a matter of some speculation! The resulting hydrogen is carried to the carbon fixation cycle, where it is added to the CO_2 molecules. And the plant simply releases the oxygen from the water as its waste gas.

But to use the energy of light, you first must trap it. Plants do this with the pigment chlorophyll, which, like all coloured substances, only absorbs light of certain wavelengths or colours, reflecting back the rest. The absorbed photons of the red and blue components of sunlight give their packages of energy to electrons in some of the atoms of chlorophyll. The green light is reflected away, making the pigment appear green. (It has been pointed out that a more efficient photosynthetic pigment would be black, allowing plants to make use of all the wavelengths of visible light, but biology is full of make-do compromises based more on evolutionary history than efficiency.)

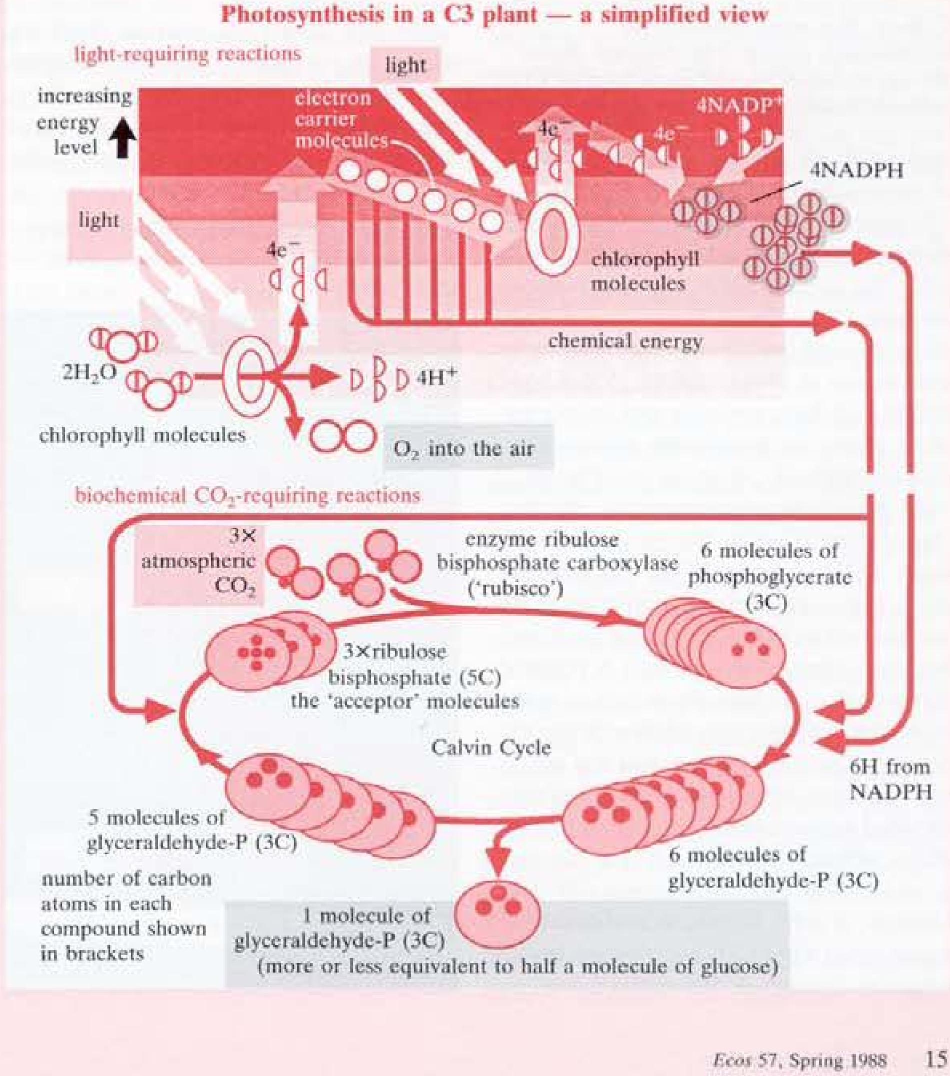
The electrons are now in a high-energy state and fly off from chlorophyll to be picked up by other compounds. But nothing lasts forever, and very rapidly they fall back to their old state, releasing their energy in a form that a biological system can put to good use. The movement of the electrons is really just a tiny electric current — only instead of moving from atom to atom in a copper wire, they pass along a chain of complex organic molecules.

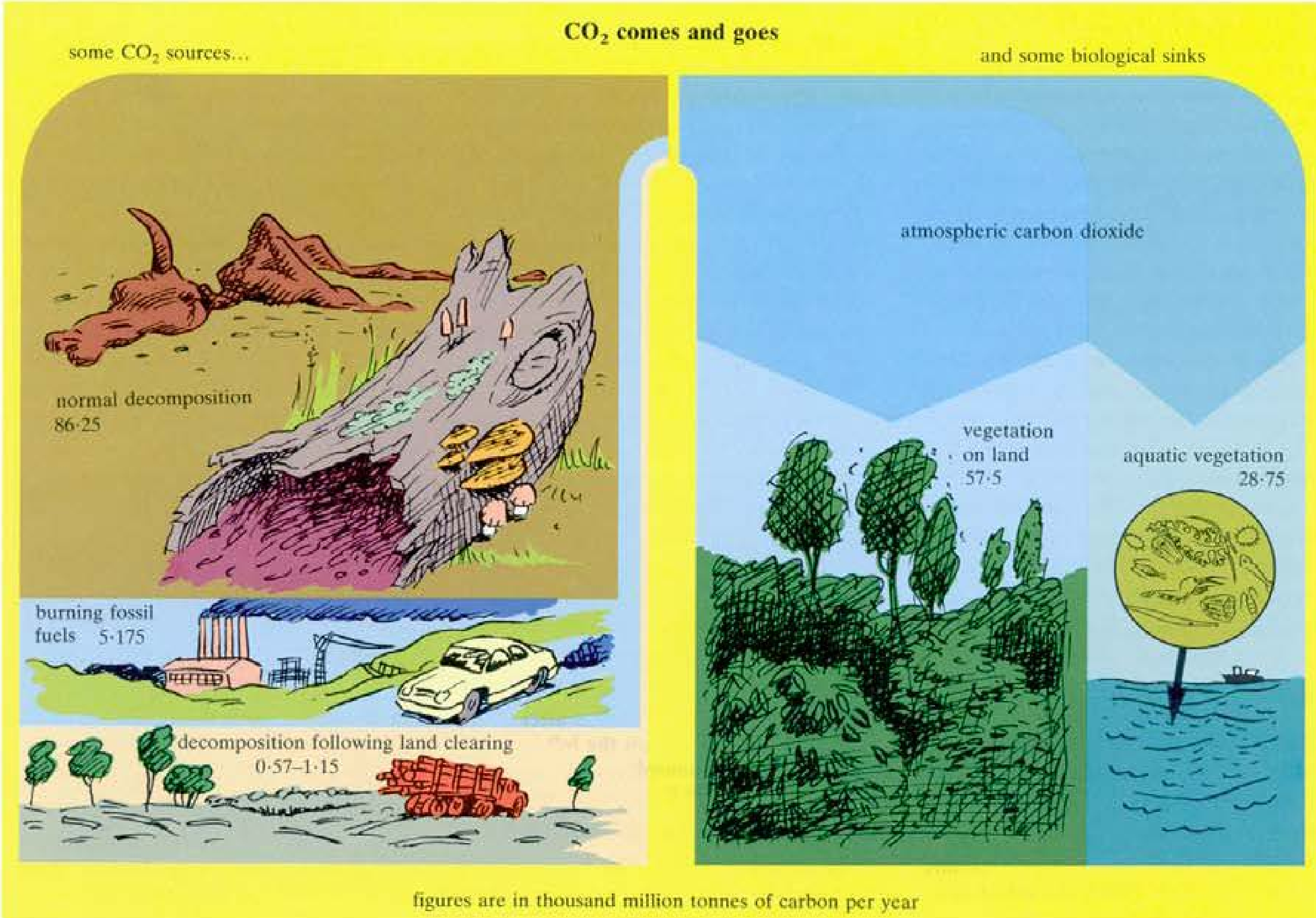
The photon-gathering chlorophyll molecules are laid out in regular arrays on thin plates, like solar panels, within a part of the leaf cell called a chloroplast. Between the plates, the chemical reactions of carbon fixation take place. Leaf cells contain many microscopically small chloroplasts, and are kept supplied with the necessary CO_2 by small pores in the leaf, which also allow oxygen to escape. Other plant cells, such as those in the roots, don't contain chloroplasts.

Not all types of photosynthesis are exactly as described above. Firstly, among the higher plants, the carbon dioxide may be fixed in two different ways, explained in the main text. And among some micro-organisms, photosynthesis may make carbohyrate without using water at all, as long as CO_2 is present. Instead of water, the hydrogens may come from hydrogen sulfide (H_2S), with the release of pure sulfur, instead of oxygen, as a waste product. Pigments other than green chlorophyll may also play a part, especially for plants living in areas — such as 30 metres down in the sea — where certain wavelengths of light are not present.

The energy of light, in association with chlorophyll and other compounds, splits water into protons (H^+), electrons (e^-), and oxygen. It also raises the energy level of the electrons, which leads to the production of the chemical energy and hydrogen needed to convert carbon dioxide to carbohydrate in the Calvin cycle.

Photosynthesis in a C3 plant — a simplified view





Carbon, like many elements, is continuously cycled. The diagram shows the approximate annual quantities of CO_2 released or taken up by various processes.

from a gas that makes up only about 0·03% of our atmosphere?

In general, plants do indeed benefit from increased levels of CO_2: the higher these rise, the greater the plants' biomass becomes. This holds true — provided other environmental factors are suitable — up to a maximum of about 1200 to 1500 p.p.m. (0·15%). In fact, tomatoes and lettuce are often grown in greenhouse atmospheres enriched with CO_2 to about these levels.

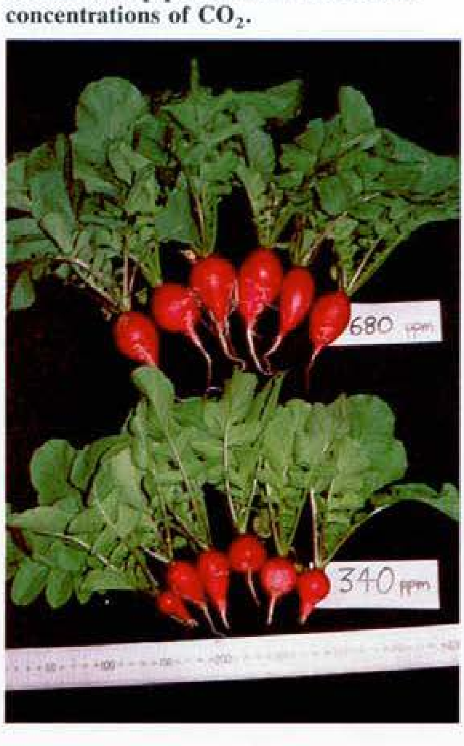
At even higher concentrations, the fertilising effect starts to fall off until, above about 5000 p.p.m. or 0·5%, CO_2 actually seems to become toxic. (The precise figures vary according to the species of plant and the environmental conditions.) A possible reason is that, at this concentration, sufficient CO_2 would go into solution in the cell sap to produce acid in quantities that would upset normal metabolism. This is because CO_2 and water react to form carbonic acid, which, although a weak acid to a chemist, is nonetheless effective biologically. For example, it is the slightly increased acidity in our blood when CO_2 accumulates in our tissues that causes us to breathe faster.

But how does CO_2 exert its fertilising effect on a plant? Several separate phenomena are involved. Most obviously, that crucial enzyme of photosynthesis ribulose bisphosphate carboxylase ('rubisco' to those who work with it) can pick up more of its substrate, because it will find more CO_2 molecules around. The plant thus fixes more carbon.

Photorespiration

The second direct effect involves some apparently inefficient biochemistry. As mentioned before, rubisco sometimes picks

Radishes (left) and barley (right) grown at normal (340 p.p.m.) and twice-normal concentrations of CO_2.



up a molecule of oxygen (O_2) rather than of carbon dioxide. The enzyme has a far greater affinity for CO_2 than for O_2, but the 600-fold greater concentration of O_2 in the air means that some oxygen molecules successfully attach. The oxygenation reaction that follows triggers a chemical path that differs from photosynthesis. It creates a molecule called phosphoglycollate, which is eventually metabolised with the associated release of a molecule of CO_2. The whole process uses up oxygen and liberates CO_2, like respiration, but takes place during the course of photosynthesis. So scientists call it photorespiration.

Despite this inefficiency, plants that photorespire can be very successful. But they may start to have problems in hot, dry conditions. With higher temperatures, rubisco becomes more likely to catalyse reactions involving oxygen; also, dry heat forces plants to close their stomata (the gas-exchange pores in the leaves) in order to conserve water. The result is a decline in the levels of CO_2 in the leaf, which makes matters worse.

Not all plants photorespire. Some have evolved a way around the problem, by using a different enzyme to 'collect' the carbon dioxide from the air. The procedure involves some rearrangements of leaf structure and biochemistry.

C3 and C4

Plants that avoid photorespiration attach a CO_2 molecule from the air to an organic molecule, containing three carbon atoms, in the leaf cells. The result — the first-formed molecule — is a four-carbon compound, and so we call this procedure the C4 pathway and its users are C4 plants. (The discoverers of these revolutionary facts about photosynthesis were Australian biochemists Dr Hal Hatch and Dr Roger Slack.) The majority of plants do not use this pathway, and they are termed C3 plants.

Of great importance is the fact that, in the C4 system, the enzyme that catalyses the first reaction with CO_2 is not affected by oxygen; consequently, no photorespiration can take place.

But the four-carbon molecule so formed will not be used in true photoysnthesis. It moves out of the mesophyll cells (the ones in contact with air via the stomata) to cells that surround the veins of the leaf. These sheathing cells contain most of the enzyme rubisco in C4 plants. Upon arrival, the four-carbon compound releases one molecule of CO_2 — in the process turning back into the original three-carbon molecule. This then finds its way back into

Two pots of sub clover 8 weeks after germination — the one on the left is receiving CO_2 at atmospheric concentration, while the one on the right receives double this amount.

the mesophyll cells to pick up more atmospheric CO_2. Rubisco, tucked away in the sheathing cells, is presented with CO_2 at a high concentration by means of this transport system, and is largely kept out of contact with atmospheric oxygen.

Of course, this shuttling between the cells uses up energy, and so most C4 plants only do well where sunshine is relatively abundant. In effect, their juggling concentrates CO_2, and avoids photorespiration, which means that they can still fix enough carbon for their needs without keeping their stomata open as much as C3 plants. They therefore lose less water and will grow faster in hot and dry conditions.

However, if air contains more CO_2 then C3 plants stressed by dry heat benefit in two ways. Firstly, the amount of carbon-wasting photorespiration will decline, as rubisco, meeting more CO_2 molecules, has fewer encounters with oxygen. Secondly — and this holds true for both types of plant — they can fix much more carbon during the time that they keep their stomata open. In other words, they can make the same amount of sugar at less cost in terms of water loss. This explains one of Dr Gifford's most important findings: that plants benefit relatively more from CO_2-enhancement if they are water-stressed. (Being already more efficient at gathering CO_2, C4 plants do not show this effect as much as their C3 counterparts.)

Dr Gifford grew wheat (a C3 plant) in dense stands and with limited water, to simulate field conditions. He found that plants grown at a CO_2 concentration of 680 p.p.m. certainly yielded more than others left at the atmospheric value of 340 p.p.m., and that a proportionately higher increase occurred in those plants that had less water available to them. The more stressed the conditions, the more dramatic was the effect. Eventually, when the available water fell to the equivalent of just 100 mm of annual rain, the plants were only able to produce grain if they received extra CO_2!

Dr Gifford speculates that the helping hand of extra carbon dioxide may also boost plants facing other environmental stresses, such as high salinity or nutrient-poor soils. But we need more research before this can be proved.

One worry remains, however: the fertilising effect doesn't just help our crops — weeds also benefit. And weeds that are C3 plants will be boosted more than crops that are C4. Fortunately, though, most of the world's worst weeds are C4 plants and many of our crops are C3; so, on average, agriculture should still benefit.

Other scientists have reported a variety of figures for the effects on yield of a doubling of CO_2, ranging from a five-fold increase to a slight decrease. The differences may reflect the extent of the genetic diversity of plants in their responsiveness to the gas, as well as environmental effects.

Transpiration

An increased concentration of carbon dioxide reduces the aperture of the

Where is all the carbon?

	atmosphere units
pre-industrial atmosphere (1860 AD)	1·0
modern atmosphere (1987)	1·3
biosphere:	
above-ground	0·9
soil organic matter	2·8
living in the ocean	<0·01
dead in the ocean	1·8
carbonates in sedimentary rocks (limestone, chalk)	67 000
fossilized organic matter:	
total in sedimentary rocks	27 000
potential 'fossil fuel'	14

Dr Gifford assigns a value of 1 to the quantity of CO_2 in the recent atmosphere before human activity changed it. This 'atmosphere unit', although about 575×10^9 tonnes of carbon, is really very little. Over the aeons, the activities of living organisms have served to 'pull' far greater quantities of carbon out of the atmosphere, depositing much of it in sedimentary rocks.

stomata, which in turn has an effect on the water loss, or transpiration, from a leaf. Plenty of other factors also affect this, ranging from light intensity to atmospheric humidity to the water status of the plant. However, Dr James Morison, a former colleague in the Division, has found that a doubling of the CO_2 concentration causes about a 40% reduction in the conductance of the stomata. (Conductance is a measure of the ability of a leaf to exchange gases or water vapour and depends on the number of stomata and their average aperture.) Reduced conductance means less transpiration.

Extra carbon dioxide has another effect relevant to this. It often causes plants to produce larger leaves, and it stimulates branching. In a range of experiments with spaced plants in a glasshouse, Dr Gifford and Dr Morison found that carbon dioxide's two effects — the increase in the leaf area and the decrease in the size of the stomata — tended almost exactly to counteract each other. This was true for a range of species and at different temperatures.

But in closed canopies of plants, the scientists think that the carbon-dioxide-stimulated increase in leaf area would be likely to compensate less because of mutual shading by the leaves, which acts to reduce transpiration further in two ways. Firstly, the leaves stay cooler, and secondly the stomata partially or completely close anyway because of the lower light intensity.

But it's possible that a global increase in CO_2 concentration could mean drier air over the land. This may 'feed back', through the reduced humidity of the air, to increase evaporation from plants and soil. Whether it would, on balance, affect regional water loss we cannot say; but it is a complicating factor of the greenhouse effect, which, remember, is already predicted to raise the average temperature of the planet — in itself expected to influence evaporation from land and sea.

A good greenhouse?

Will all plant life, and therefore our agriculture, be improved in a greenhouse world? The answer is not simple. When we look beyond the direct impact on plants due to increasing carbon dioxide and consider the true greenhouse effect — that is, a higher temperature brought about by the accumulation of various gases in the atmosphere — the news is mixed.

Perennial plants tend to increase their productivity with higher temperatures, but a 1°C rise produces a bigger result in cold climates than in warm ones. This suggests that in the tropics the CO_2 fertilising effect on C3 plants will be of more benefit than the greenhouse temperature increase, but in high latitudes the opposite will hold true.

As warm conditions act to speed up plant growth and development, annual plants will mature and die more quickly. But because they reach maturity in less time, they intercept less light energy all told, and for some crops this means a lower yield.

Wheat provides a good example. As Dr Gifford has shown, a simple doubling of CO_2 will give approximately a 30% increase in the yield. But, with his Divisional colleague Dr Maarten Stapper, he estimates that a 2°C temperature rise will completely cancel out this gain if the wheat is irrigated.

For wheat grown in dry areas of Australia, the projected story differs. In this case, early maturing means that the plants form their ears before the summer drought takes hold. As a result, they have more water available during that critical phase, which compensates for the shorter growing period and so, in the end, yields are not greatly affected. Also, the CO_2 fertilising effect itself will, in relative terms, help plants in dry areas more than in wetter ones.

The future

The concentration of atmospheric CO_2 has been steadily rising for about a century, from a pre-industrial level of approximately 280 p.p.m. to 350 p.p.m. now. And the rate of increase is itself increasing! During this time we have seen an expansion in the yield of our crops and, although this is often put down to genetic and agronomic improvement, some of the credit could go to the fertilising effect.

If, in the future, we burn all the fossil fuels we can readily extract, then we could see a six-fold increase in the global level of CO_2. But assuming that even humanity's careless abandon is unable to create such monstrous pollution, we are still likely to face a doubling. What should we do?

It seems sensible to start looking for differences in responsiveness to the CO_2 fertilising effect, and breed cultivars to take greater advantage of the future atmosphere. We could also put greater emphasis on C3 crop species, as the effect will benefit them more.

All in all, Dr Gifford believes it is probably safe to conclude that a global increase in the CO_2 concentration, acting alone, will have a positive impact on food production — a silver lining indeed. But don't carry on consuming petrol and burning gas with only this in mind. The greenhouse that benefits plants has an ugly side: it could precipitate dramatic changes in climate and rainfall patterns, and eventually cause a rise in sea level that could have serious economic effects around the world's coastlines (see *Ecos* 53). Perhaps we are better off as we are.

Roger Beckmann

More about the topic

Exploiting the 'fertilising' effect of higher levels of atmospheric carbon dioxide. R.M. Gifford. In 'Proceedings of Climate and Food Security: an International Symposium, New Delhi, India, February 6–9, 1987', ed. S.K. Sinha. (IRRI: Los Baños, Philippines 1988.)

Plant growth and water use with limited water supply in high carbon dioxide concentrations. J.I.L. Morison and R.M. Gifford. *Australian Journal of Plant Physiology*, 1984, **11**, 361–4.

Stomatal sensitivity to carbon dioxide and humidity. J.I.L. Morison and R.M. Gifford. *Plant Physiology*, 1983, **71**, 789–96.