

without the need for bulky cooling arrangements<sup>8</sup>. Another possible application for arrays of photonic lasers would be in multi-colour light-emitting displays, in which the colour (wavelength) of the light 'pixels' could be varied easily.

The possible applications of photonic-bandgap structures are not restricted to telecommunications. The ability to control the emission process could lead to lasers that have intrinsically quantum-optical properties — for example, single-photon sources that could be used in experiments to explore the quantum nature of light. Such quantum lasers could find eventual applications in quantum cryptography and optical quantum computers. And if a laser with a near-zero threshold could be produced, then the 'spare' heat from the human body

might provide enough energy to switch it on, suggesting considerable economic and ecological implications. The work reported by Zhou *et al.*<sup>4</sup> and others is an important step in this direction — and the long-term prospects for photonic-bandgap lasers are surely bright. ■

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Plant biology

# Coping with human CO<sub>2</sub> emissions

Laura Serna and Carmen Fenoll

For two centuries, a natural experiment has been showing how increasing atmospheric CO<sub>2</sub> affects plants. Laboratory work provides pointers as to how they will respond in the future.

The industrial revolution in the western world had enormous socioeconomic effects — but it also unwittingly started a global experiment that has now been running for two centuries. One of the unforeseen consequences of the industrial revolution was a steady increase in the amount of carbon dioxide in the atmosphere. Plants responded by having fewer stomata — paired 'guard' cells, found mainly on the surface of leaves, that control the uptake and release of gases. Enrichment of atmospheric CO<sub>2</sub> continues. But how will plants respond in the future? Water loss and CO<sub>2</sub> uptake occur primarily through the stomata, so a drastic further decrease in their numbers would impair processes such as transpiration and photosynthesis.

On page 713 of this issue<sup>1</sup>, Gray *et al.* tackle this problem. They show that the small mustard plant *Arabidopsis thaliana* is endowed with a gene, christened *HIGH CARBON DIOXIDE (HIC)*, that prevents changes in the number of stomata in response to further atmospheric CO<sub>2</sub> enrichment. This finding not only provides new evidence linking CO<sub>2</sub> and stomatal development, but also opens the way to understanding how plants will cope with anthropogenic CO<sub>2</sub> emissions in the future.

An inverse relationship between stomatal density and atmospheric CO<sub>2</sub> levels, from pre-industrial to modern times, has been demonstrated by analyses of specimens collected from herbaria over the past 200 years<sup>2</sup>. Laboratory experiments in which plants

were grown at pre-industrial CO<sub>2</sub> levels confirmed the relationship between CO<sub>2</sub> concentration and both stomatal density<sup>2,3</sup>

and stomatal index<sup>2</sup>. (The stomatal index is given by [stomatal density/(stomatal density + epidermal-cell density)] × 100, where epidermal cells include guard cells as well as others that constitute the outer covering of leaves.) But several experiments have shown that enrichment of the present atmospheric CO<sub>2</sub> levels induces only minor further changes in stomatal density<sup>2,3</sup> and index<sup>2</sup>. The implication is that the response of the stomatal index to CO<sub>2</sub> in many plant species is now close to saturation. It seems that plants may continue to make enough stomata, regardless of how much more CO<sub>2</sub> is dumped into the atmosphere by humans.

The results of Gray *et al.*<sup>1</sup> lend support to this view. The authors' laboratory experiments show that roughly doubling the current atmospheric CO<sub>2</sub> levels has no effect on the stomatal index in the leaves of at least one strain of *Arabidopsis*. They also show that plants with a loss-of-function mutation in the *HIC* gene exhibit a large increase in this index when grown at the higher CO<sub>2</sub> concentration. The implication is that the unmutated *HIC* gene represses this increase in stomatal index in response to atmospheric CO<sub>2</sub> enrichment. An increase in stomatal density might well be as much of a problem as a decrease, because water loss might be too high.

So, what does *HIC* do? Mutant plants with defects in stomatal patterning have been identified previously<sup>4–7</sup>. But, unlike

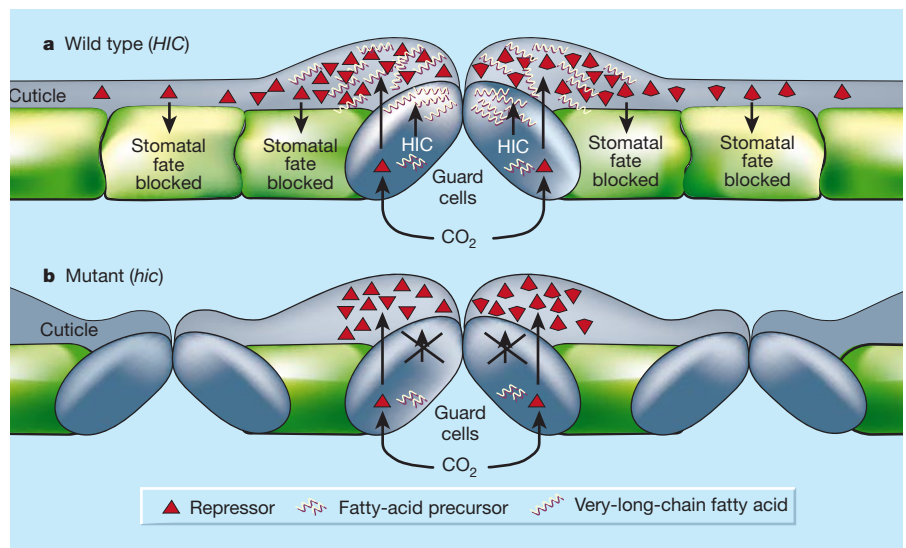


Figure 1 Plant stomata and anthropogenic carbon dioxide emissions. Over the past 200 years, the number of plant stomata (each of which consists of a pair of guard cells, delimiting a pore for gas exchange) has decreased in response to increasing CO<sub>2</sub> levels<sup>2,3</sup>. This trend may not continue in the future. Gray *et al.*<sup>1</sup> show that the stomatal index remains the same in normal *Arabidopsis* plants in response to CO<sub>2</sub> concentrations double those of today, but increases in plants with a mutant *HIC* gene. The authors suggest that the normal *HIC* gene negatively regulates stomatal development at the higher CO<sub>2</sub> concentrations, as shown here. a, The normal *HIC* gene may encode an enzyme involved in the synthesis of very-long-chain fatty acids, deposited at the surface of the guard cells. These fatty acids might be needed for the diffusion of a molecule — stimulated by high CO<sub>2</sub> concentrations — that can reach neighbouring epidermal cells and repress their ability to develop into stomata. b, In *hic* mutant plants, the relevant fatty acids are not made. Diffusion of the repressor is therefore impaired, so it cannot reach all its target cells, which develop into stomata.

these plants, the *hic* mutants do not have stomata that directly contact one another<sup>1</sup>. So it seems that the normal *HIC* gene is not required to ensure that a full complement of non-stomatal cells surrounds each stoma.

Gray *et al.* next cloned the *HIC* gene, and found that its sequence has many bases in common with the *Arabidopsis KCS1* gene, which codes for a 3-keto acyl coenzyme A synthase<sup>8</sup>. In plants, such enzymes are involved in synthesizing fatty acids with very long chains, which are important in the cuticle waxes on the surface of epidermal cells<sup>9</sup>. The authors worked out the amino-acid sequence of the normal and mutant *HIC* proteins, and propose that the mutant protein should not be able to synthesize a component or components of the waxy cuticle of guard cells. They suggest that these alterations might result in an increase in the stomatal index in response to atmospheric CO<sub>2</sub> enrichment.

But how might an altered cuticle influence epidermal development in such a way that the stomatal index is increased? Gray *et al.* put forward a possible model (Fig. 1): in the mutant plants, the change in the cuticle overlying the guard cells interferes with its permeability to a hypothetical substance that is stimulated by doubled CO<sub>2</sub> levels, blocking the effects of this substance. In normal plants this substance might diffuse from the cuticle above the guard cells to nearby epidermal cells, there repressing the development of extra stomata. Very limited diffusion of the repressor might occur in *hic* mutant plants, and this might be sufficient to prevent the formation of stomata adjacent to one another. As the authors point out<sup>1</sup>, if this model fits reality, we might be close to showing that a lateral inhibition process operates during the establishment of stomatal patterns at CO<sub>2</sub> levels that are double those of today.

To investigate further whether cuticular waxes influence stomatal development, Gray *et al.* measured the stomatal index of *eceriferum-1* and *eceriferum-6* mutants, which have alterations in wax composition<sup>10</sup>. Both mutants have higher stomatal indices than do wild-type plants at current CO<sub>2</sub> atmospheric levels<sup>1</sup>. This finding establishes a link between the lipid composition of the cuticle and the development of stomata. Work on these and other mutant plants is already revealing that cuticle lipids are important in processes involving cell–cell interactions at plant surfaces<sup>11</sup>. But the question of whether these lipids simply help these processes — providing an adequate environment for other molecules to operate — is still open.

The main message of Gray *et al.*'s work<sup>1</sup> is that plants seem to be well armed to cope with a further enrichment in atmospheric CO<sub>2</sub> (at least until CO<sub>2</sub> levels are double those at present). Genes such as *HIC* should

ensure that, at high CO<sub>2</sub> concentrations, changes in stomatal indices are kept to a minimum. But *HIC* does not seem to be necessary to regulate stomatal development at current CO<sub>2</sub> levels, as mutant *hic* plants showed no stomatal defects at such concentrations<sup>1</sup>. Future challenges include not only unveiling the components of the *HIC*-mediated developmental signalling pathway, but also understanding the mechanisms that allowed plants to decrease their number of stomata as CO<sub>2</sub> levels rose from pre-industrial to present-day levels. In any case, it seems that further increases in CO<sub>2</sub> emissions might not drastically alter stomatal density. But be on guard — the global experiment is still running. ■

Geochemistry

## Mantle recycled in Sardinia

Barry B. Hanan

The origin of the 'EM-1 signature' evident in certain basalt rocks is a long-standing puzzle. Comparison of data from Pitcairn Island and Sardinia may shed some light on the enigma.

Oceanic 'large igneous provinces' (LIPs) are areas of the sea floor where the ocean crust is especially thick — 30 km or more. During the plate tectonic process of subduction along island arcs, when sea floor sinks back down into the mantle, LIPs are thought to remain at the surface because of their comparative buoyancy and to accrete to the continental crust. On page 701 of this issue, however, Gasperini *et al.*<sup>1</sup> propose that at least some LIP ocean floor has been recycled back into the deep mantle during plate subduction and has reappeared in the Logudoro lavas of northwestern Sardinia. This work bears upon a long-standing geochemical puzzle: the origin of the 'EM-1 signature' in certain rocks.

Large igneous provinces (such as the Ontong–Java plateau) and 'hotspot' volcanoes (such as Pitcairn, Tristan da Cunha, Iceland and Hawaii) both form from plumes of hot material rising up through Earth's mantle. Mantle plumes consist of a huge head (500–2,000 km in diameter) on top of a tail (100 km wide) of hot upwelling deep mantle. Ocean LIPs are thought to result from lavas erupted during melting of the head in an early stage of plume development, producing massive amounts of lava the size of continents. By contrast, hotspot volcanoes form over more mature plumes, after dispersion of the plume head, by melting of plume tails.

Normal ocean crust is created at mid-ocean spreading centres, where upwelling mantle decompresses and melts. This crust, 4–8 km thick, consists of pillow basalts — lavas chilled by sea water — that are fed from below by dykes emanating from a magma

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chamber and are overlain by deep-sea sediment. Oceanic LIPs, which may constitute up to 10% of the ocean floor, have a similar structure to normal ocean crust but are as much as five times thicker<sup>2</sup>.

The Earth's mantle contains several isotopically 'extreme' components that contribute to the sources of ocean basalts<sup>3,4</sup>. Three of these components have been identified in the radiogenic isotope signatures of hotspot volcanoes. They are known as HIMU (high <sup>238</sup>U to <sup>204</sup>Pb) and EM-1 and EM-2 — EM standing for 'enriched mantle', meaning enriched in certain elements. These components are thought to represent ancient recycled oceanic crust and its overlying sediment that has undergone varying degrees of hydrothermal alteration on the sea floor (see ref. 5 for review).

Gasperini *et al.*<sup>1</sup> point out that the geochemistry of the Logudoro lavas resembles that of Pitcairn, an EM-1-type hotspot island in the Pacific Ocean. The EM-1 mantle source is especially puzzling because its geochemistry is consistent not only with contributions from recycled, ancient crust and deep-sea sediment<sup>6</sup>, but also with ancient lithosphere from beneath the continents<sup>7</sup>. Because EM-1 signatures are evident in LIP basalts associated with plume heads rising beneath the continents<sup>7</sup>, there is the question of whether the EM-1 signature is due to contamination of plume heads by subcontinental lithosphere or whether it derives from the original plume source. Solving this enigma is fundamental to deciphering the origin of the isotope components of the mantle<sup>8</sup>.

The Pitcairn and Logudoro lavas both