

Respiration in the balance

John Grace and Mark Rayment

Models of how forests will respond to climate change usually assume that carbon dioxide output from decomposing organic matter will increase with global warming. That assumption may be wrong.

Each year, the world's vegetation absorbs about 60 billion tonnes of carbon by photosynthesis and releases a similar — but not exactly equivalent — amount by respiration¹. These fluxes of carbon are large, dwarfing the 6.5 billion tonnes emitted by the burning of fossil fuel. Most of the terrestrial photosynthesis and respiration is carried out by ecosystems that produce woody material — forests and savannahs (Fig. 1). The respiratory flux is partly from the plants themselves, but about 50% is from microbial decomposition of the organic matter that the plants have produced. There is a large stock of this organic matter in the soil, much of it in the form of very old and only slowly degradable residues of lignin (the main constituent of the cell walls of woody plants).

From the global patterns of CO₂ concentration, it seems that terrestrial photosynthesis and respiration are not in balance^{2,3} — photosynthesis appears to exceed respiration by 2 billion tonnes of carbon per year³. It is now possible to measure these fluxes at specific forest sites⁴. The measurements show quite clearly that old and undisturbed forests, as well as middle-aged forests, are net absorbers of CO₂ (refs 5–7). The reason may be increased CO₂ fertilization (CO₂ stimulates photosynthesis) together with increased deposition of anthropogenic nitrogen (which also acts as a fertilizer)⁸. This is good news: it means that forests are serving as a carbon sink, providing a global environmental service by removing CO₂ from the atmosphere and thus reducing the rate of CO₂-induced warming.

However, the forest sink may not persist. In all forests studied so far, the net gain of carbon is the small difference between the two huge numbers representing photosynthetic gains and respiratory losses. In the future 'greenhouse' world, photosynthesis is likely to increase with rising CO₂ levels and nitrogen deposition, enhancing the sink strength. However, as every physiologist knows, respiration rates increase sharply with temperature⁹. So it is generally believed that respiration — both of the vegetation itself and of microbial decomposition of organic matter — will increase with global warming. The commonly held view, then, now enshrined in models of global change, is that the carbon sink provided by forests will weaken, and that in the long term the world's forests may

Ecosystem type	Carbon production (g × 10 ¹⁶)
Forest	23.25
Savannah	18.61
Temperate grassland	4.39
Tundra arctic/alpine	0.95
Desert and semidesert scrub	1.35
Extreme deserts	0.06
Bogs, unexploited peatland	0.68
Cultivated land	6.77
Other	3.80
Total	59.86

Figure 1 Carbon production by terrestrial ecosystems. (Adapted from ref. 14.)

eventually become a source of carbon to the atmosphere.

Two papers on pages 858 and 861 of this issue^{10,11} make us think otherwise. Giardina and Ryan's results¹⁰ corroborate and extend findings from Finnish soils¹² suggesting that, over long periods of time (decades), decomposition of organic matter is not very sensitive to temperature. It seems that short-term warming experiments showing a rise in respiration do not capture the long-term characteristics of its response to rising temperatures.

But the results reported in the second paper, which come from a network of CO₂ flux-measurement stations set across Europe's forests, are even more surprising. Valentini and colleagues¹¹ show that respiration is a more important component of the carbon balance in northerly latitudes despite the low temperatures there, and that it is really respiration, not photosynthesis, that varies over the latitudinal band from Iceland to Italy.

Are the results of Valentini *et al.* likely to be general? Despite the great difficulty of sampling forests that are truly representative over the whole of Europe, we suspect that they do indeed reveal a real trend with latitude. We await results from a similar network of stations in the United States, which may confirm this trend. Meanwhile, we know that carbon fluxes in the tropics are larger than those in temperate and northern forests^{5,6}. But there is not enough information yet to comment on the long-term effects of temperature on the carbon balance, and further data are needed from rainforests and savannahs to complete the global picture.

Why should soil respiration be higher in a colder climate? Perhaps it is because the soil in the north is wetter for longer, and so microbes that are adapted to work at low

temperature are active for most of the year. In more southerly latitudes, by contrast, the microbes become inactive for much of the year when the soil is dry. Or perhaps the more northerly ecosystems contain much carbon as organic matter which has accumulated in the soil over previous, colder periods, and is only now decomposing as the soil warms in response to climate change.

To illustrate the importance of these papers to our understanding of the future of the terrestrial carbon sink, we set parameters for a simple ecosystem model of conifer forest using routines and procedures described elsewhere¹³. For case 1 we adopted the commonly held view and assumed that the ecosystem respiration will rise in line with long-term increases in temperature. For case 2 we modified the model and assumed that ecosystem respiration would continue to respond to daily and seasonal variations in temperature, but would be insensitive to longer-term temperature changes. In both cases we ignored any age-related changes in the forests, as this would complicate the picture needlessly.

The result (Fig. 2) clearly shows that the

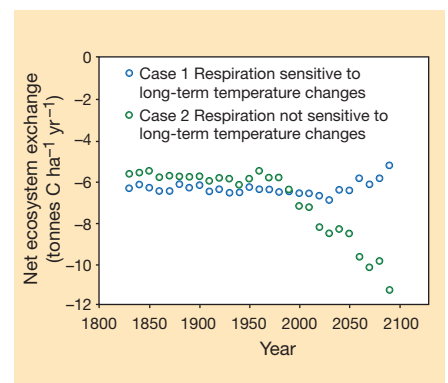


Figure 2 A long-term prediction of the net ecosystem exchange of carbon in a generic northern European forest. Data plotted are ten-year means of model output, where respiration is (case 1) or is not (case 2) sensitive to long-term changes in temperature. The possibility of case 2 applying stems from research reported in refs 10–12. In case 1 the sink diminishes; in case 2 the sink strengthens to over 10 tonnes of carbon per hectare per year. A more negative number means an increasing uptake of carbon by the forest. (Model run with climate data output from a general circulation model, using scenario IS92a of the International Panel on Climate Change¹⁵.)

assumption made about the temperature sensitivity of ecosystem respiration has a profound effect on the long-term future of the forest carbon sink in coniferous forest. If case 1 is correct, the sink diminishes, and the forest becomes less effective at removing CO₂ from the atmosphere; if case 2 is correct, the effect of an increasing rate of photosynthesis is not masked by an increasing respiration rate, and the forest becomes increasingly more effective as a sink for atmospheric CO₂.

In any case, the results from these two papers^{10,11} should send a powerful message to those working with models of global vegetation change. Setting the parameters for soil respiration models using only the results of short-term experiments may be quite misleading. When respiration models are eventually fully coupled to models of climate change, the resulting positive feedback between respiration and temperature that magnifies global warming may proceed only

for a limited time — until the easily decomposed soil organic matter is depleted. Does this mean that the doomsday view of runaway global warming now seems unlikely? We hope so. ■

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Cognitive neuroscience

Seeing in the sound zone

Michael Merzenich

How is the development of the processing capabilities and organization of the brain's cerebral cortex controlled? Intrinsic mechanisms (such as genetically encoded developmental programmes) and extrinsic inputs (such as the things we see and hear, and the ways that this information is encoded by specific discharges within particular sensory systems) both have a say. But to what extent can the developmental pathways be overruled by inputs from the outside world? Two fascinating papers by Sur and colleagues, on pages 841 and 871 of this issue^{1,2}, provide some of the most compelling evidence yet for the exquisite sensitivity of cortical development to external cues.

How does one even start to determine the relative contributions of external and internal factors to cortical development? Ferrets have proved a useful model animal, in part because they are born before their development has progressed too far. Over the past decade, Sur and co-workers have been perfecting an experimental approach that consists of surgically manipulating the nerves that feed into different parts of the cortex of very young ferrets. Specifically, the nerves from the retina (which normally lead to a subcortical region, the visual thalamus, which in turn feeds into the primary visual cortex, or V1) are redirected to grow into the auditory thalamus (which feeds into the primary auditory cortex, or A1). The auditory thalamus itself is deprived of its normal auditory inputs in this model.

In early experiments^{3,4}, Sur and col-

leagues showed that this 'rewiring' procedure results in the emergence of a functional V1 in a cerebral cortex zone that was otherwise destined to develop into primary auditory cortex. The new visual cortex has a topographic organization that parallels that in normal V1. Moreover, different neurons in this rewired cortical zone — like those in normal V1 — are selective for differently orientated visual stimuli. The normal

organization of A1, in contrast, goes awry: the A1 territory is taken over by visual inputs. Such experiments have provided important evidence that the organization and responsiveness of different cortical regions can be shaped by the particular patterns of neuronal discharge that result from neuronal stimulation by different inputs — in this case, by retinal versus cochlear (auditory) inputs.

Sur and colleagues' latest papers^{1,2} advance this theory by several crucial steps. First, Sharma, Angelucci and Sur¹ show that particular higher-order features seen in normal V1 emerge in the rewired visual cortex (Fig. 1). These features are called 'visual orientation columns': each consists of a group of neurons that share a preference for visual stimuli with a particular orientation. The layout of these columns provides a basis for representation of important spatial characteristics of visual stimuli. The 'pinwheel' organization of these columns (Fig. 1) in the rewired animals resembles that in V1. The authors go on to show that horizontal connections — links between separate columns that represent corresponding stimulus orientations — emerge in the rewired auditory cortex, just as in normal V1. These horizontal connections and organizational structure have no equivalents in the normal A1. All of these studies^{1,3,4} convincingly show that much of what typifies the functional organization of V1 can be generated within A1 by delivering retinal inputs to A1 through the auditory thalamus.

But the story does not end there. Von Melchner, Pallas and Sur² demonstrate that rewired animals show behavioural responses to visual stimuli that are presented only to the neurons feeding into the rewired

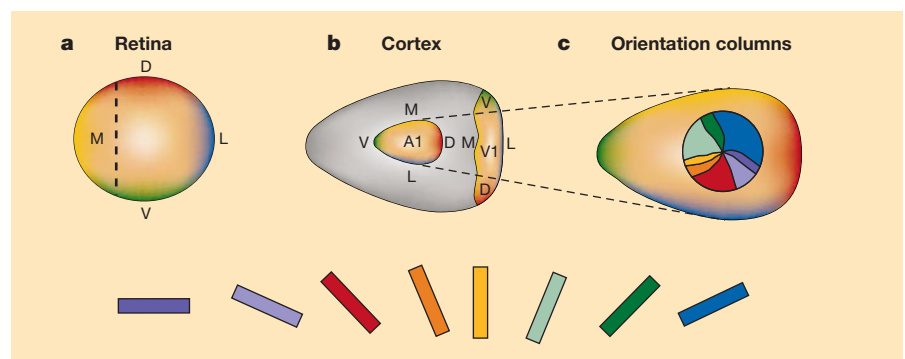


Figure 1 Rewiring the brain. Sharma *et al.*¹ and von Melchner *et al.*² have redirected neurons that normally lead to the visual thalamus (and then the primary visual cortex, or V1) into the auditory thalamus (and then the primary auditory cortex, or A1). a, The retina, showing its medial (M), dorsal (D), lateral (L) and ventral (V) dimensions. b, In the 'rewired' cortex, a 'retinotopy' (a map of neuronal inputs from different parts of the retina to different parts of the cortex) forms in the A1 area. (In some ferrets, in which V1 and the visual thalamus were left intact, a normal retinotopic map also forms in the V1 area.) c, An enlarged view of the rewired A1. Features called 'pinwheels', seen in V1 in normal ferrets, also form in the rewired cortex. Each colour in a pinwheel represents a group of neurons that respond to a particular orientation of visual stimulus. Thus, a functional V1 is formed in the A1 area in the rewired cortex of these ferrets. (The key along the bottom relates to the pinwheel diagram in the centre of c. So, for example, the dark yellow colour in the pinwheel identifies a group of neurons that respond to a vertically orientated stimulus.)