

Figure 2 How the bipolar dendrites of coincidence detection neurons, and the mapping of synaptic inputs from each ear to different dendrites, improve sound localization. That improvement is achieved using the nonlinear mechanism (saturation) inherent in the summation of excitatory synaptic inputs, and the exaggeration of this nonlinear loss when the inputs are clustered on one dendrite. **a**, When the input arrives from only one ear, reaching only one dendrite, the consequence of nonlinear summation in that dendrite is that less depolarizing synaptic current is generated. The resulting synaptic potential is too small to generate spike firing in the output axon. **b**, When inputs arrive simultaneously from the two ears and are segregated on different dendrites, nonlinearity in the summation of the synaptic inputs is less significant. The resulting synaptic potential is above the threshold and it gives rise to a spike being fired in the axon.

inputs from one ear are likely to saturate the dendritic potential, a mistimed input from the other ear (to another, unsaturated, dendrite) becomes very effective in depolarizing the axon and may result in an inappropriate firing of the cell. Indeed, with increasing sound frequency, the task of phase-locking between the input sound and the timing of spikes in the auditory nerve is more difficult and the precision of spike timing falls off (that is, the spikes ‘jitter’). One way to counteract the possibility of erroneous CD firings is to reduce saturation at the dendrites in high-frequency CD cells, which can be done by making the dendrites shorter. With shorter dendrites, a lower voltage is required at the synaptic site for triggering a spike in the output axon. That is because less current is lost to the other dendrite and more is available to reach the threshold for spike firing; the lower the dendritic voltage, the smaller the saturation at the dendritic site. Obviously, the benefits of nonlinear addition are less for shorter dendrites. So Agmon-Snir and colleagues’ model predicts an optimal length for a given frequency, with shorter dendrites for higher frequencies, and experiments⁵ show that this is indeed the case.

What of other types of neuron with dendrites, such as those depicted in Fig. 1 — do they use similar principles to enrich their computational capabilities? The example provided by Agmon-Snir *et al.* is a rare one, because we usually don’t know the specific computational function of a given type of neuron. So the modelling studies of the past 30 years need pushing further to continue to provide insights into the possible computational power of neurons with dendrites (for reviews see refs 6–10). The new work³ was

inspired by these studies, and it is likely that the computational module isolated in the auditory neurons for improving coincidence detection might be used in other dendritic neurons with input segregation, such as cortical pyramidal neurons and cerebellar Purkinje cells, perhaps as part of a more complex computational system.

Climate change

The carbon equation

David S. Schimel

Following the signing of the Climate Convention in Rio in 1992, and the subsequent conference in Kyoto late last year, there is a pressing need to find out more about the relationship between anthropogenic emissions of the main greenhouse gas, CO₂, and the resulting atmospheric concentrations. In its reports^{1,2} dealing with 1994 and 1995, the Intergovernmental Panel on Climate Change (IPCC) provided estimates for a wide variety of scenarios, to give policymakers some information on anthropogenic emissions consistent with the aim of stabilizing atmospheric CO₂ at a range of levels (from 350 to 1,000 parts per million by volume).

Uptake or release of CO₂ from the world’s oceans and terrestrial ecosystems is central to understanding the relationship between emissions of CO₂ and its atmospheric levels. The IPCC 1994 assessment, however, conducted only a preliminary examination of how altered CO₂, climate and ocean circulation might affect that relationship. Now, in papers on pages 245 and 249 of this issue,

But the findings of Agmon-Snir *et al.* go beyond providing one convincing example of dendritic function, for they also bear on a controversy between two schools of thought. These are the ‘individualists’, who believe in the functional primacy of the neuronal details (the specific dynamics of synapses, the fine morphology of the dendrites, the exact timing of spikes); and the ‘socialists’, or ‘connectionists’, who believe that the characteristics of neuronal society owe little to the properties of its individual components. Agmon-Snir *et al.* have demonstrated the power of the individual, but we eagerly await more studies that tie the variety of dendritic morphologies to their specific function. □

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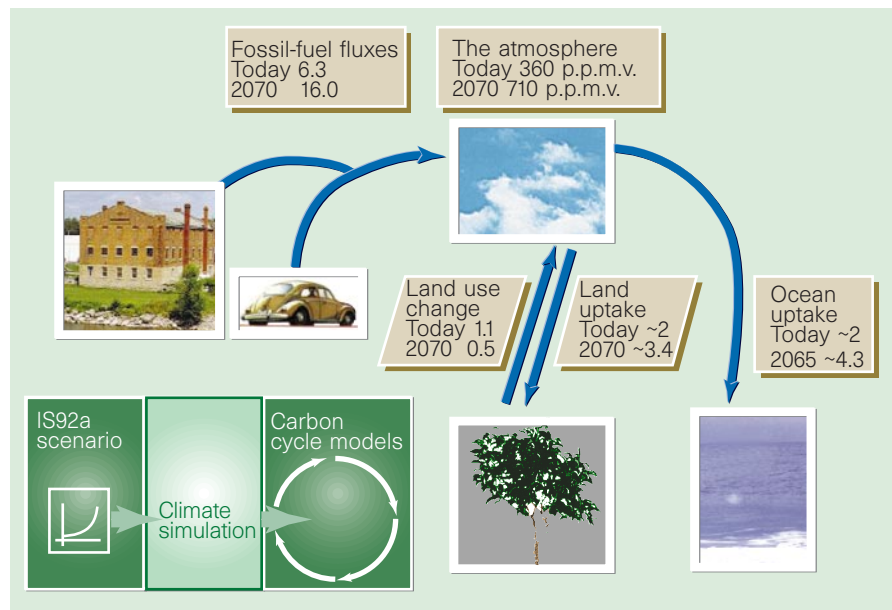


Figure 1 Present-day fluxes of anthropogenic CO₂ compared with estimated fluxes for the year 2070 (or 2065 in the case of Sarmiento *et al.*³). Units are 10¹⁵ g yr⁻¹ unless stated otherwise; p.p.m.v., parts per million by volume. The estimates for 2070 (2065) are taken from IPCC IS92a figures, or in the case of land uptake⁴ and ocean uptake³, are from models of the response of land and oceans to climate change using IS92a as input; IS92a, or IPCC Scenario 92a, gives projections of increasing emissions of CO₂ from use of fossil fuels, assuming moderate growth rates. The inset at bottom left indicates how scenarios of increased anthropogenic emissions of CO₂ feed into climate simulations and then models of the carbon cycle.

demonstrates the maturation of models of plant physiological processes at large scales.

Sarmiento *et al.*³ address the effects of environmental change and marine processes on carbon fluxes in the oceans. The modelled effects occur through changes in salinity, changes in sea-surface temperatures and (via a sensitivity study) changes in the efficiency of biotic uptake on future carbon storage in the oceans. This model links the biota to carbon storage through the availability and utilization of phosphorus as a limiting nutrient, using carbon-to-nutrient (Redfield) ratios. Modelled productivity is controlled by anomalies in the supply of nutrients to the surface ocean, which are caused by changes in circulation or in the efficiency of nutrient use in marine ecosystems. In their somewhat contrived but informative sensitivity analysis, Sarmiento *et al.* show that marine biological changes could have larger effects on ocean carbon storage than alterations in ocean dynamics.

That the fluxes predicted by these models differ from IPCC baseline estimates¹ has serious implications for policy designed to stabilize the concentration of trace gases in the atmosphere. If policies reducing emissions are implemented and CO₂ uptake in the oceans or on land is less than predicted, concentrations will exceed targets. Conversely, if the system is more efficient at sequestering CO₂ than predicted, unnecessary mitigation costs could be incurred. Given the central role of fossil energy, errors in predicting the carbon budget could come at high economic

cost. Both of these studies used only one climate scenario, corresponding roughly to a growth of CO₂ of 1% per year, so the uncertainties in the biogeochemistry they incorporate are amplified by uncertainties in the climate models themselves.

The juxtaposition of these two papers highlights a major difference in approach between marine and terrestrial science. Sarmiento and colleagues' model assumes that productivity is basically linked to nutrient supply and use, and neglects the details of planktonic physiology and population dynamics. Cao and Woodward's model is largely driven by changes to physical resources — light, heat, water and CO₂ — and emphasizes plant physiology and its diversity between life-forms. Yet terrestrial ecosystems are influenced by nutrient supply (as well as internal recycling and adjustment, for instance changes to plant or soil C:N ratios). In particular, further analysis of Cao and Woodward's carbon budget implies that there would be a significant reorganization of the global nitrogen cycle.

Cao and Woodward calculate an atmosphere-land-ecosystem carbon flux of about 1.1 × 10¹⁵ g yr⁻¹ in the 1980s and of 3.2 × 10¹⁵ g yr⁻¹ in the middle of the twenty-first century. Their estimates go back to 1861, and the overall result is a sink of 300 × 10¹⁵ g between then and 2070. The sink is divided about 2:1 between vegetation and soils. This implies a corresponding sink for nitrogen, because organic matter contains, stoichiometrically, both carbon and nitrogen. The sink of nitro-

gen in soils alone, taking a mean of 10:1 for the C:N ratio of soils, implies a minimum sequestration of nitrogen of 30 × 10¹² g yr⁻¹ to sustain today's carbon flux and of 100 × 10¹² g yr⁻¹ in the future (slightly less if C:N ratios respond to increased CO₂). Storage in vegetation, which is lower in nitrogen than soils, will increase these demands slightly.

These nitrogen fluxes are proportionately quite large relative to today's nitrogen budget (anthropogenic inputs to natural ecosystems today are about 50–75 × 10¹² g yr⁻¹), and are unlikely to be sustained in the long term by internal readjustments. Although increased biological nitrogen fixation could make up some of the balance, the implied nitrogen flux to land ecosystems in the years 2050–2070 is more than twice today's estimated rate. Although Cao and Woodward do not directly model nitrogen inputs, their results imply that there will be a significant demand on nitrogen to sustain extra CO₂-stimulated photosynthesis. Some terrestrial ecosystems may be limited by phosphorus, but Alan Townsend of the University of Colorado (personal communication) has calculated an upper bound for carbon storage in tropical forests from phosphorus deposition of no more than 0.1 × 10¹⁵ g yr⁻¹, or roughly a tenth of the Cao and Woodward flux — again, this is a large discrepancy to be accounted for by internal readjustments.

Study of the interaction of the biogeochemical cycles⁶ has been eclipsed by the stunning increases in our understanding of terrestrial photosynthesis, but results such as Cao and Woodward's imply a need for a renewed research emphasis on the global cycles of nitrogen, phosphorus and other nutrients to better predict what will happen to levels of atmospheric CO₂. Likewise, the sensitivity of Sarmiento and colleagues' model to nutrient use implies a need for substantially increased biological detail, along the lines of Cao and Woodward's approach, in large-scale ocean models. Taken together, these two studies bring a renewed sense of urgency to research on the future behaviour of the Earth System, especially the coupling of anthropogenic greenhouse gases to the climate and carbon systems. □

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