

Box 1. Superinfection: just one complicating factor

Gandon *et al.* [a] assume that an invading parasite immediately replaces the already resident parasite, so that, within their models, parasites compete for host occupancy. Within this model, any reduction in overall transmission level reduces the advantage to the parasite of exploiting the host rapidly, because the likelihood is reduced that an infection will be terminated prematurely by a superinfection.

The assumption that superinfections replace existing parasite clones was also made by many early malarialogists [b], however, the orthodoxy on this issue for many years was the idea that superinfecting parasites behave independently of pre-existing parasite populations [c]. Now, although we can use molecular techniques to type parasites, it is clear that superinfection is frequent, but that the infections are certainly not independent of each other. Reality is somewhere between the two extremes. The resulting competition among malaria parasites within the individual host complicates any realistic model for the evolution of virulence.

References

- a Gandon, S. *et al.* (2001) Imperfect vaccines and the evolution of pathogen virulence. *Nature* 414, 751–756
- b Sergent, E. and Parrot, L. (1935) L'immunité, la prémunition *et al.* résistance innée. *Arch. Inst. Past. Alg.* 13, 279–319
- c MacDonald, G. (1950) The analysis of infection rates in diseases in which superinfection occurs. *Trop. Dis. Bull.* 47, 907–915

What would be the implications of vaccination against blood-stage antigens if they play a role in cross protecting against invading clones? It is not easy even to predict the immediate consequences, which might well depend upon whether vaccination tends to eliminate the existing parasites, or to boost immune responses to the existing infections. The evolutionary implications are at least as unclear (Box 1).

It is commendable that Gandon *et al.* have stimulated thinking about the possible evolutionary consequences of malaria vaccines. But it is important to

remember that their model is only one of many that are possible and that it might be a better model for simpler systems (such as viral pathogens) than it is for malaria. Unexpected effects of vaccination are probable when imperfect malaria vaccines are introduced on a large scale. The secondary effects of vaccination should certainly be monitored closely and, as Gandon *et al.* recommend, intrinsic growth rates of parasites are one parameter that should not be forgotten. But, it is not at all obvious that the predictions that they make will prove accurate.

References

- 1 Gandon, S. *et al.* (2001) Imperfect vaccines and the evolution of pathogen virulence. *Nature* 414, 751–756
- 2 Anderson, R.M. and May, R.M. (1982) Coevolution of hosts and parasites (Pt 2). *Parasitology* 85, 411–426
- 3 Ebert, D. (2001) The evolution and expression of parasite virulence. In *Evolution in Health and Disease* (Stearns, S., ed.), pp. 161–172, Oxford University Press
- 4 Bojang, K.A. *et al.* (2001) Efficacy of RTS,S/AS02 malaria vaccine against *Plasmodium falciparum* infection in semi-immune adult men in The Gambia: a randomised trial. *Lancet* 358, 1927–1934
- 5 Genton, B. *et al.* A recombinant blood-stage malaria vaccine reduces *Plasmodium falciparum* density and exerts selective pressure on parasite populations in a Phase I/IIb trial in Papua New Guinea. *J. Infect. Dis.* (in press)
- 6 Chotivanich, K. *et al.* (2000) Parasite multiplication potential and the severity of falciparum malaria. *J. Infect. Dis.* 181, 1206–1209
- 7 White, N.J. (1998) Malaria pathophysiology. In *Malaria: Parasite Biology, Pathogenesis and Protection* (Sherman, I.W., ed.), pp. 371–385, American Society for Microbiology
- 8 Smith, T. *et al.* (1999) Consequences of multiple infection with *Plasmodium falciparum* in an area of high endemicity. *Parasitologia* 41, 247–250

Tom Smith

Swiss Tropical Institute, Socinstrasse 57,
PO Box, CH-4002, Basel, Switzerland.
e-mail: Thomas-A.Smith@unibas.ch

Meeting Report

New advances in carbon cycle research

Josep G. Canadell and Diane Pataki

The 6th International Carbon Dioxide Conference was held in Sendai, Japan, from 1–5 October 2001.

Although the Intergovernmental Panel on Climate Change (IPCC) Third Assessment Report (TAR) was published recently [1] with the latest assessment of our understanding of the global carbon (C) cycle, there is already a wealth of new information available. The 6th International Carbon Dioxide Conference provided a venue for scientists to present new findings that contribute to our understanding of the current and future C cycle.

Contemporary carbon sources and sinks: patterns

The Northern Hemisphere net C sink is currently relatively well constrained, but its longitudinal distribution is largely unknown. New analyses from multiple inverse models show that the Northern Hemisphere land sink during the 1990s was distributed quite evenly among North America (0.83 Pg C y⁻¹), Europe (0.62 Pg C y⁻¹) and Asia (0.61 Pg C y⁻¹). Surprisingly, boreal Asia accounted for a sink of 0.52 Pg C y⁻¹, while boreal North America was a net C source of 0.26 Pg C y⁻¹ (K. Gurney, Colorado State University, Fort Collins, CO, USA).

Less is known about the sink strength of the tropics, but it is thought to be large enough to counteract the 1.6 Pg C y⁻¹ that are emitted because of tropical deforestation. Thus, inverse model calculations show a fairly unconstrained net balance of zero for the region between 15°N and 15°S. Even less is known about its longitudinal distribution, but ground-based estimates indicate that ~50% of the sink is in Amazonia (0.75 Pg C y⁻¹), and the other half is distributed equally between tropical Africa and south-east Asia (Y. Malhi, University of Edinburgh, UK).

The contemporary budget and distribution of C sinks and sources in the

oceans is better constrained, although the role of the Southern Ocean (SO) as a sink is still controversial. Atmospheric inverse modelling shows that SO is a C source of $\sim 0.5\text{--}1\text{ Pg C y}^{-1}$, whereas atmospheric inverse models constrained with oceanic pCO_2 climatology show that the SO was a small source during the 1980s and a small sink during the 1990s. Large-scale biogeochemical ocean models show that the SO is currently a relatively large sink ranging from -0.5 to -1.0 Pg C y^{-1} . Results from recent ship cruises show that SO was a source of $\sim 0.1\text{ Pg C y}^{-1}$ for year 2000 (N. Metzl, University P. and M. Curie, Paris, France).

Contemporary carbon sources and sinks: interannual variability

Some of the disagreements regarding the strength and distribution of global and regional sinks are being resolved by a better understanding of the year-to-year dynamics caused by climatic forcing. The dynamic ranges from $<1\text{ Pg C y}^{-1}$ to $\sim 3\text{ Pg C y}^{-1}$ for the global sink, and alters C sinks to C sources in regional balances. Changes driven by the El Niño Southern Oscillation (ENSO) appear to have a large influence on CO_2 growth rate. The study of multiple atmospheric species signatures, particularly the $\text{CH}_4\text{:CO}_2$ ratio, indicates that increased biomass burning caused by drought during El Niño years is probably the single largest cause of changes in the C growth rate. Other mechanisms, such as increased CO_2 flux from heterotrophic respiration and CH_4 flux from wetlands, might also have an influence (R. Langenfelds, CSIRO Atmospheric Research, Aspendale, Australia).

Analyses of the CO_2 concentrations, $^{13}\text{C}\text{:}^{12}\text{C}$ ratio and $\text{O}_2\text{:N}_2$ ratio confirm that, during the 1990s, the terrestrial biosphere was the dominant source of variation in CO_2 growth rate, and global land and ocean C sinks averaged 2.1 Pg C y^{-1} and 1.0 Pg C y^{-1} , respectively. These measurements incorporate corrections for O_2 outgassing owing to increasing ocean stratification (R. Keeling, Scripps Institution of Oceanography, La Jolla, CA, USA).

Interannual variability is even larger at the regional level. For example, the change from net C sink to net C source for some Arctic tundra ecosystems in Alaska between 1999 and 2000 was due to the influence of weather conditions on the

balance of winter C efflux and summer C uptake (Y. Harazono, National Institute for Agro-Environmental Sciences, Tsukuba, Japan).

Processes and stability of C sinks

Little is known about the mechanisms responsible for the magnitude and spatial distribution of terrestrial sinks. Increased understanding of the interannual variability provides some useful information, but mechanisms relevant to longer timeframes (decades to centuries), and therefore to long-term sink stability, are often quite different. There are various types of sink mechanism: (1) increasing net primary production (NPP) (e.g. CO_2 and N fertilization); (2) decreasing disturbances (e.g. fire suppression); (3) recovery from past disturbances (e.g. forest regrowth in abandoned agricultural land); and (4) other mechanisms, such as sediment burial, land fills and long-lived wood products (C.B. Field, Carnegie Institution of Washington, Stanford, CA, USA). Surprisingly, only 30% of the 0.5 Pg C y^{-1} USA C sink [2] is due to forest growth and only 25% of the total is due to human activity. This indicates that the capacity of terrestrial sink manipulation to reduce atmospheric CO_2 growth is limited. Out of 180 Pg C that, historically, have been emitted from land-use change, no more than 30 Pg C can be sequestered back to into vegetation and soils.

Many of the mechanisms responsible for the current sink have reached their maximum sink capacity, and their strength is decreasing over time. Others mechanisms will peak depending on future management strategies, but all will subsequently saturate or decrease over the coming decades–centuries.

New approaches

Global and regional C measurements must be tightly linked. In addition, no single

component of the experimental, observational and modelling platforms (e.g. process studies, CO_2 measurement networks and satellite data) can credibly lead to a comprehensive explanation of the controls and quantities of the C cycle at different spatial and temporal scales. Therefore, we have seen the recent introduction of approaches that take advantage of complementary and mutually constraining measurements. For example, a method has been developed to estimate regional C fluxes for Australia using field measurements of NPP, satellite data, atmospheric surface CO_2 concentrations, and a process-based model. The estimated net ecosystem production ranged from a source of $+0.12\text{ Pg C y}^{-1}$ to a sink of -0.13 Pg C y^{-1} for 1990–1998, with a reduced coefficient of variance when constrained by the multiple measurements (Y.-P. Wang, CSIRO Atmospheric Research, Aspendale, Australia).

Other important methodological developments will make use of the soon to be available global mapping of CO_2 concentrations from space-borne instruments (e.g. NASA EOS–Aqua). Although the measurements are of relatively low precision compared with land-based methods, they are unbiased and global in coverage, which will substantially improve inverse modelling results. Currently, only ~ 100 stations produce CO_2 concentration data over the land and ocean surface (S. Denning, Colorado State University, Fort Collins, CO, USA). In addition, satellite measurements of CO_2 tropospheric profiles contain crucial longitudinal information that improves derived regional surface fluxes by 45–60%, even assuming a 1-ppm measurement uncertainty (B.C. Pak, University of California, Irvine, CA, USA). Other more sophisticated assimilation–prediction

Box 1. Future research needs

- Rationalization of the global carbon (C) observing system (CO_2 measurements, eddy covariance C fluxes, field experiments, etc.) with expansion to key regions (e.g. Southern Ocean and tropical Asia).
- Data harmonization, calibration and instrument improvements.
- Development of new platforms to use multiple constraints from several data sources, and design of new model–data fusion schemes, including the use of global low-precision CO_2 retrievals from space-borne instruments.
- Improvement of C flux estimates from land-use change with appropriate spatial coverage.
- Understanding of the effects of fire, climatic variability, and the nitrogen cycle (deposition and nutrient limitation) on the C cycle.
- Moving beyond diagnosis into prediction with a better understanding of the mechanisms determining C sinks and sources.

schemes are being developed that are expected to revolutionize the approaches for measuring contemporary C sources and sinks with a built-in predicting capacity. This is the case of the scheme using atmospheric transport and process-based terrestrial ecosystem models being developed by P. Rayner (CSIRO Atmospheric Chemistry, Aspendale, Australia).

In the future, our predictive capacity will be greatly improved by the integration of multiple scales and methods of C cycle research into

comprehensive regional and global frameworks (Box 1). There is a need to expand measurements into poorly constrained regions whilst providing global intercalibration and data harmonization, and emphasizing process studies in key areas of uncertainty. We thank the hosts and sponsors of the 6th CO₂ Conference for the opportunity to further our synthetic understanding of the global C cycle.

References

- 1 IPCC (2001) *The Intergovernmental Panel on Climate Change (IPCC)*

Third Assessment Report, Cambridge University Press

- 2 Pacala, S.W. *et al.* (2001) Consistent land- and atmosphere-based US carbon sink estimates. *Science* 292, 2316–2320

Josep G. Canadell*

GCTE/IGBP IPO Office, CSIRO Sustainable Ecosystems, Canberra, Australia.

*e-mail: Pep.Canadell@gcte.org

Diane Pataki

GCTE/IGBP Focus 1 Office, University of Utah, Salt Lake City, UT, USA.

Like minds: evolutionary convergence in nervous systems

Steven M. Phelps

The Karger Workshop, 'Evolutionary convergence as a tool for neuroscience,' was held by the J.B. Johnston Club at an annual satellite meeting associated with the Society for Neuroscience in San Diego, CA, USA on 9 November 2001.

The J.B. Johnston Club (JBJC), a group devoted to the study of brain evolution, convenes annually with the Society for Neuroscience conference. The first day of the 2001 JBJC meeting was a workshop on evolutionary convergence in nervous systems*. Talks reviewed evidence that convergence is common among nervous systems, that convergent neurobiological features can inform our understanding of behavioral evolution, and that such features can provide insight into how brains work.

Examples of convergent nervous systems were abundant. Kiisa Nishikawa (Northern Arizona University, Flagstaff, AZ, USA) reviewed the prey-catching mechanisms of frogs that have repeatedly evolved an inertial tongue elongation mechanism that uses the jaw to propel and extend the tongue like an elastic whip [1]. The mechanism requires acute sensory feedback, which has been accomplished by innervating the tongue with sensory nerve fibers. Frogs that do not use inertial elongation have a hypoglossal

nerve that innervates tongue and hyoid muscles to drive their contraction, but does not contain sensory fibers to provide feedback. In one family of inertial elongators, the bufonid frogs, sensory fibers from the glossopharyngeal nerve now innervate the tongue. In Ranidae, by contrast, a comparable sensory feedback is conveyed through fibers derived from the cervical spinal cord. There are often many ways to achieve a given phenotype, and the details of convergence can be clarified by the examination of proximate mechanisms of trait expression.

The workshop's keynote speaker, Greg Wray (Duke University, Raleigh, NC, USA), emphasized the importance of proximate mechanisms and thorough taxonomic sampling in identifying and understanding convergence. He reviewed the evolution of several developmental mechanisms, including the role of the homeobox gene *engrailed* in the patterning of nervous systems. In both arthropods and vertebrates, *engrailed* is involved in organizing a bilaterally symmetric nervous system: in mice, there are two *engrailed* genes that define a boundary between the developing midbrain and hindbrain [2]; in *Drosophila*, as in other arthropods, *engrailed* is expressed in serial, paired ganglia [3]. In the brittle star *Amphipholus squamata*, the gene is expressed in the paired ganglia of the radial nerve, which run along each arm [4]. In spite of similar expression patterns in these taxa, Wray argued that

the *A. squamata* profile represents convergence rather than homology. The basal echinoderm nervous system lacks bilateral symmetry in radial nerve ganglia: although the role of *engrailed* in neurogenesis seems to be homologous, its expression in the paired ganglia of brittle star arms and arthropod bodies does not. The combined analysis of *engrailed*, *orthodonticle* and *distalless* genes across echinoderm classes makes a compelling case for the evolutionary lability of developmental mechanisms.

The role of developmental control genes resurfaced in one of several talks on sensory processing. Curtis Bell (Oregon Health and Sciences University, Portland, OR, USA) discussed the repeated evolution of sensory nuclei that resemble the cerebellum, a vertebrate hindbrain structure that governs balance. He noted that the ability of the gene *Fgf8* to induce development of novel cerebellum-like structures [5] might facilitate the evolution of comparable circuitry in other sensory systems. Other speakers included Jon Kaas (Vanderbilt University, Nashville, TN, USA), who reviewed the emergence of specialized visual cortex in squirrels and primates. Catherine Carr and Daphne Soares (University of Maryland, College Park, MD, USA) presented data suggesting that birds and mammals have converged on common mechanisms for timing auditory events – a process needed for sound localization. Heather Eisthen's (Michigan State University,

*Acknowledgements. The workshop was organized by Kiisa Nishikawa and Heather Eisthen and was sponsored by Karger Press. Proceedings of the workshop will be published in *Brain, Behavior and Evolution* in summer 2002.