NEWS & VIEWS

CARBON CYCLE

Sink in the African jungle

Helene C. Muller-Landau

Apparently pristine African tropical forests are increasing in tree biomass, making them net absorbers of carbon dioxide. Is this a sign of atmospheric change, or of recovery from past trauma?

The lush vegetation of tropical forests is a large and globally significant store of carbon[1]. Because tropical forests contain more carbon per unit area than any alternative land cover, cutting them down releases carbon into the atmosphere. For the same reason, growing forests take up carbon from the atmosphere. Of course, trees cannot grow for ever, and neither can forests: in the absence of disturbances that kill trees en masse — such as fires, hurricanes or logging — every forest will eventually reach a point at which tree growth and death are in equilibrium, and at which the average change in tree carbon stocks is zero.

It is thus surprising that undisturbed tropical forests currently do not seem to be at equilibrium. If you measure the size of trees in a given area, calculate their carbon stocks, and then repeat the process some years later, you will on average find that the forest holds more carbon than it did before. This was first reported for Amazonian tropical forests[2], and on page 1003 of this issue Lewis *et al.*[3] show that African forests also have increasing stocks of tree carbon.

So how much carbon are we talking about? Using data collected in Africa between 1968 and 2007, the authors find that trees have added an average of 0.63 tonnes of carbon per hectare each year. Given that approximately half the dry matter in trees is carbon, the amount of wood added annually in each hectare of African forest is equivalent in mass to a small car. For comparison, the average rate of carbon accumulation in tropical forests around the globe was 0.49 tonnes of carbon per hectare per year[2–4]. Extrapolating from their data[3] by assuming parallel changes in the carbon pools of roots and dead trees, Lewis *et al.* estimate that 'old-growth' tropical forests are taking up 1.3×10^9 tonnes of carbon per year worldwide.

There are two possible explanations for this finding. One is that the tropical forests that we think of as intact actually suffered major disturbances in the not-too-distant past, and are still in the process of growing back[5]. This recovery process is known as succession, and takes hundreds — or even thousands — of years. Succession involves not only initial growth to full canopy height, but also subsequent gradual shifts in species composition. The past disturbances could have been natural or anthropogenic; possible explanations include droughts and fires related to huge El Niño events, and changes in land use that allowed previously cleared land to revert to forest[5].

A. CANELA/PHOTOLIBRARY

Figure 1 | Getting bigger. Lewis *et al.*[3] show that apparently undisturbed African tropical forests are currently increasing in tree biomass each year, and act as carbon sinks. But it is impossible to say how long this will continue.

In fact, palaeoecological and archaeological evidence increasingly documents the long disturbance histories of today's 'undisturbed' tropical forests[6]. There have been many large fires in Amazonian forests over the past few millennia, the timings of which are related to both climate and the size of human populations[7]. Far from being pristine wildernesses little influenced by their human inhabitants, many areas were cleared or otherwise intensively used in centuries past[8]. Given the timescales of tropical-forest succession, these disturbances are almost certainly contributing to carbon accumulation in many tropical forests today.

The second explanation for Lewis and colleagues' findings[3] is that tropical forests have been knocked from their previous equilibrium by global climate and/or atmospheric change[9], so that they are currently in transition to a higher carbon state. Perhaps, for example, the increase in atmospheric carbon dioxide is effectively fertilizing tropical tree growth. Under these circumstances, if tree mortality doesn't keep pace with increases in growth, then trees will on average grow larger before they die (Fig. 1), and tree carbon stocks will increase[10]. Carbon stocks in mature tropical forests vary enormously depending on climate, soil type and topography; temporal changes in climate and resource availability would therefore be expected to have parallel influences in the long run.

The two mechanisms that might account for Lewis and colleagues' observations[3] would be expected to produce different spatial and temporal patterns of carbon uptake by trees, but our current knowledge does not allow us to predict what these patterns are, or to say which mechanism is operating in Africa. Over the course of succession, tree carbon stocks increase at an ever-slower rate as stands age. Thus, we

expect tree carbon stocks and their rate of change, and stand age, to be closely related within any given forest type. In temperate and boreal forests, where stand age is generally well known, carbon stocks and fluxes do indeed show a strong relationship with stand age, even at ages many consider to be old-growth[11]. Examination of these relationships in tropical forests is stymied not only by lack of information about how long ago disturbances occurred, but also by limited knowledge of how growth rates and equilibrium carbon stocks are affected by rainfall, soils and other factors.

One might suppose that predictions based on the global-change hypotheses are more straightforward — after all, atmospheric CO_2 concentrations are rising equally everywhere. In fact, the effects of CO_2 fertilization on tree growth are expected to depend strongly on other factors that vary greatly among forests, especially the availability of soil nutrients[1]. And if changing climate (rather than rising atmospheric CO_2) is affecting the carbon flux of tropical forests, then the outcomes will differ depending on local changes and the local baseline.

It is likely that both succession and global change have a role in explaining tropical-forest growth, with varying importance at different sites. Where recovery from disturbance drives tropical-forest change, associated changes in species composition would be expected. A study published last year[4] found that tree species with slower growth rates are disproportionately increasing in biomass in nine out of ten 'undisturbed' tropical forests around the globe, as would be expected during succession. Yet Lewis *et al.*[3] find no relationship between a species' wood density and the rate of change of its population across their African plots.

A better understanding of tropical-forest carbon dynamics is clearly needed to determine the causes of the observed increases in tropical tree carbon stocks — and, more critically, to predict the future trajectory of these stocks under global change. Furthermore, we must look not only at the trees[3], but also at the soil: tropical-forest soils hold at least as much carbon as the trees. Unlike tree carbon stocks, soil carbon stocks can potentially increase indefinitely. But the prevailing prediction is that increasing temperatures will speed decomposition and reduce soil carbon stocks.

In the future, will tropical trees and soils act as carbon sinks, thereby slowing atmospheric and climate change? Or will altered climates turn them into carbon sources that accelerate further change? Standardized assessments of the main carbon pools and fluxes of tropical forests around the world — and their proposed drivers — are needed to document and understand the current trends, to inform predictive models, and ultimately to answer these pressing questions. ■

Helene C. Muller-Landau is at the Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Balboa, Ancon, Panamá, República de Panamá.
e-mail: mullerh@si.edu

1. Solomon, S. D. *et al.* (eds) *Climate Change 2007: The Physical Science Basis* (Cambridge Univ. Press, 2007).
2. Phillips, O. L. *et al. Science* **282,** 439–442 (1998).
3. Lewis, S. L. *et al. Nature* **457,** 1003–1006 (2009).
4. Chave, J. *et al. PLoS Biol.* **6,** e45 (2008).
5. Wright, S. J. *Trends Ecol. Evol.* **20,** 553–560 (2005).
6. Clark, D. A. *Biotropica* **39,** 4–19 (2007).
7. Bush, M. B., Silman, M. R., McMichael, C. & Saatchi, S. *Phil. Trans. R. Soc. Lond. B* **363,** 1795–1802 (2008).
8. Mann, C. C. *Science* **321,** 1148–1152 (2008).
9. Lewis, S. L. *Phil. Trans. R. Soc. Lond. B* **361,** 195–210 (2006).
10. Muller-Landau, H. C. *et al. Ecol. Lett.* **9,** 589–602 (2006).
11. Luyssaert, S. *et al. Nature* **455,** 213–215 (2008).

NEUROSCIENCE

Good and bad cell death

Donald W. Nicholson

Neurodegeneration often has disease connotations. However, it is also a developmental process for fine sculpting of the nervous system. One signalling cascade might mediate the process in both circumstances.

A major driver of neurodegeneration in Alzheimer's disease is thought to be plaques of amyloid-β peptides. These 40–42-amino-acid fragments form when the transmembrane amyloid-β precursor protein (APP) is degraded by the enzymes β- and γ-secretase. In addition to amyloid-β peptides, degradation of APP results in the formation of other peripheral fragments[1]. Perhaps unsurprisingly, given the compelling link between the deposition of amyloid-β peptides and the development of Alzheimer's disease[2,3], these additional fragments have been outshone and have received scant attention. But on page 981 of this issue, Nikolaev and colleagues[4] report that one oft-neglected fragment — the soluble amino-terminal portion of APP (N-APP) — has a crucial role in fine-sculpting of the nervous system during development, and possibly in disease-associated neurodegeneration as well.

In the nervous system, cell death is a surprisingly common and immensely robust process, especially during development, when productive neural circuits are reinforced and non-productive ones are eliminated. The neurons that fail to establish appropriate links with other neurons are culled mainly by apoptosis, a process that has the cell 'commit suicide' and then package up its residual bits for recycling. Those neurons that forge essential connections are protected from apoptosis by 'trophic' proteins such as nerve growth factor (NGF).

To engage other cells, neurons sprout axonal extensions, which, when necessary, are also pruned by similar, although not identical, mechanisms. So, just as Michelangelo described his technique for the creation of masterpieces such as the *Pietà* saying, "Every block of stone has a statue inside it and it is the task of the sculptor to discover it", the intricate biochemical processes of biogenesis and death determine the formation, maintenance and capabilities of the nervous system.

One approach by which to study these intricate, sophisticated and little-understood processes is to grow neurons in culture and then induce apoptosis by withdrawing NGF. Using this method in three types of spinal-cord neuron, Nikolaev *et al.*[4] find that the apoptotic machinery of these cells responds to NGF withdrawal as expected — neurons commit suicide or axons degenerate. In each case, however, initiation of apoptosis seems to depend on the presence of the 'death receptor' DR6.

Members of the death-receptor family sense

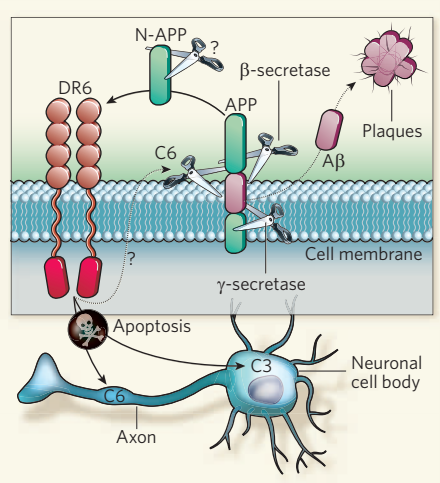

Figure 1 | Neurodegeneration signalling cascade. The transmembrane amyloid-β precursor protein (APP) is routinely cleaved by β- and γ-secretase enzymes to generate both amyloid-β peptide (Aβ) and the amino-terminal portion of APP (N-APP). The soluble N-APP may then undergo further processing before binding to the death receptor DR6. Nikolaev *et al.*[4] find that DR6 responds to interaction with N-APP by engaging and activating key mediators of apoptotic cell death: caspase-3 (C3) in the neuronal cell body and caspase-6 in axons. Caspase-6 (C6) can also cleave APP near the β-secretase target site, potentially contributing to the formation and/or amplification of this apoptotic circuit.