tissue (gross calcification) within both coral species increases at higher atmospheric CO_2 levels. Therefore, the net slowdown in skeletal growth by these corals under increased CO_2 occurs not because they are unable to calcify, but rather because their unprotected skeleton is dissolving faster (Fig. 1). The mussel *Mytilus galloprovincialis* and the limpet *Patella caerulea* showed similar trends in their ability to accrete shell under high-CO_2 conditions.

As net calcification represents the balance between the formation of new shell or skeleton beneath healthy tissue and the dissolution of exposed shell or skeleton, the impact of ocean acidification on a creature's net calcification may be largely controlled by the status of its protective organic cover. This varies both among and within species owing to genetic differences, as well as to the health, nutrition and handling of individual specimens. The findings of Rodolfo-Metalpa and colleagues may thus explain some of the variability in responses observed in previous experiments.

The authors also make the potentially important observation that the positive relationship between CO_2 and gross calcification for the coral *B. europaea* and the mussel *M. galloprovincialis* in early to mid-summer becomes negative following late summer warming of the Mediterranean Sea. They conclude that the combination of warming and acidification was simply too much for these calcifiers to overcome.

Although external organic layers should help protect calcifiers' shells and skeletons from corrosive sea water once they have formed[2], their presence alone cannot explain how organisms continue calcifying — often at higher rates — in undersaturated conditions. Rodolfo-Metalpa and colleagues propose that some creatures must use bicarbonate ions (HCO_3^-) in

their calcification process[8], which, unlike carbonate ions (CO_3^{2-}), actually increase under conditions of increased CO_2. But how, precisely, might calcifiers use HCO_3^-?

As atmospheric CO_2 levels increase, so too does the concentration of HCO_3^- in sea water and in organisms' calcifying fluid, which for some organisms appears to be derived from sea water[9]. Direct and indirect evidence suggests that many marine calcifiers use proton (H^+) pumps or ATPase Ca^{2+}–H^+ exchange mechanisms to elevate the pH of their calcifying fluids up to two units above that of the surrounding sea water[10–16]. Elevated pH at the site of calcification causes HCO_3^- in the calcifying fluid to spontaneously dissociate into H^+ and CO_3^{2-}, the latter of which combines with Ca^{2+} ions to form $CaCO_3$, which is organized into shell or skeletal structures via molecular and/or organic templates[15] (Fig. 1).

Recently published pH measurements of the calcifying fluid of another temperate coral, *Astrangia poculata*, under normal and acidified conditions reveal that this coral targets a fixed external:internal H^+ ratio (approximately 85:1), regardless of external seawater pH[12]. The inset of Fig. 1 illustrates the predicted change in calcifying fluid saturation state (Ω_A; proportional to the concentration of CO_3^{2-} and Ca^{2+} ions) for three hypothetical calcifiers that target the low (7:1), moderate (45:1) and high (300:1) external:internal H^+ ratios for atmospheric CO_2 conditions (pCO_2 400–2,850 µatm) encompassed by the Rodolfo-Metalpa *et al.* study. Critically, the response of calcifying fluid Ω_A to moderately increased atmospheric CO_2 levels (pCO_2 ~400–900 µatm) should be neutral-to-positive for calcifiers that maintain external:internal H^+ ratios greater than approximately 80:1. This may explain how the organisms investigated in the study by Rodolfo-Metalpa and colleagues were able to

continue accreting new material — in some cases at elevated rates — in undersaturated, high-CO_2 conditions.

Nevertheless, the distinction between gross and net calcification becomes increasingly irrelevant at threshold levels of atmospheric CO_2, as dissolution begins to dominate the calcification equation. Rodolfo-Metalpa and colleagues touch on this midway through their report, where they casually mention that at pH 7.3, colonies of one coral species had completely dissolved within five months of transplantation. This understated observation may prove to be the report's most dire: at certain CO_2 levels, even thick-skinned calcifiers can't protect themselves from the effects of ocean acidification. ❐

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ECOLOGY

Prime time for microbes

As atmospheric CO_2 increases, more plant litter is expected to enter the soil, stimulating turnover of organic matter and release of carbon. New field data show that this will intensify the terrestrial carbon cycle in the long term, and may counterbalance expected gains in carbon storage.

Yakov Kuzyakov

Photosynthesis, and consequently net primary production, is limited by the atmospheric concentration of carbon dioxide (CO_2). Future increases in atmospheric CO_2 (ref. 1) are thus expected to boost plant biomass, assuming

a plentiful supply of the limiting nutrients nitrogen[2] and phosphorus. Indeed, over recent decades rising atmospheric CO_2 concentrations together with human-induced global eutrophication[3] have bumped up global biomass production[4].

This increase in primary production attributed to increased CO_2 concentrations has led to expectations that many ecosystems will act as vast stores of carbon, sequestering CO_2 that would otherwise accumulate in the atmosphere. Writing in
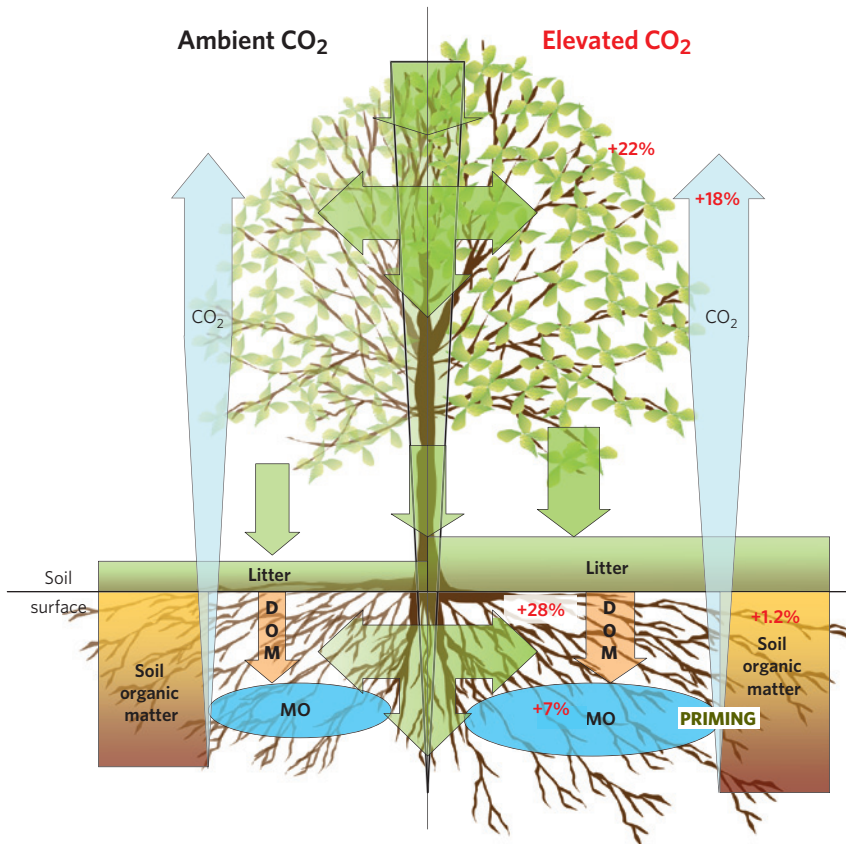
Figure 1 | The impact of increased above- and below-ground plant litter input on carbon cycling. Increased CO_2 concentrations boosts productivity, which increases the carbon input onto and into the soil (right). This increases the carbon being released back to the atmosphere in a positive feedback loop. Sayer *et al.* show that the addition of litterfall primes microorganisms (MO) for long-term acceleration of SOM decomposition[5]. The resulting CO_2 release further challenges the assumption that tropical soils will act as carbon reservoirs as atmospheric concentration of CO_2 increases. Average percentage effects of increased atmospheric CO_2 concentrations (to between 430 and 750 ppm) in various ecosystems from experimental studies are presented in red[2]. The percentages refer to: above-ground biomass; root biomass; microbial carbon; soil carbon; and CO_2 flux to the atmosphere from soil respiration. DOM, dissolved organic matter.

Nature Climate Change, Emma Sayer and colleagues[5] challenge that assumption. They report that increased litterfall can stimulate the release of soil organic carbon in tropical forests, creating a positive feedback that ultimately lowers the carbon sequestration potential of tropical forest ecosystems.

The consequences of increased organic carbon input — for example in the form of plant litter — for an ecosystem depend crucially on the interactions between its carbon pools. For the sake of simplicity, most global climate models assume no such interactions. In a system without those interactions, amplified litter inputs are partitioned between soil organic matter (SOM) pools, microbial biomass, and outputs (such as emitted CO_2 and leaching of dissolved organic carbon) in

the same proportions as under ambient conditions. For such a system, the pools already present in the soil, such as SOM and microbial biomass, preserve their usual turnover rates, and their relative contributions to atmospheric CO_2 concentrations therefore remain constant. The consequences of increased organic carbon input — including plant litter — for such ecosystems are predictable (at the most basic level), but have not been not confirmed experimentally[5,6].

In the real world, however, ecosystems do have interacting carbon pools and an increase in litter input results in a more complex outcome. Sayer and co-workers looked at the outcome of boosted biomass production in a tropical lowland forest in Panama over a six-year period. They found that doubling the litter input

accelerated the turnover of SOM in a tropical forest[5]. But as increased litter input does not affect SOM turnover directly, other indirect mechanisms must be responsible. There are two mechanisms that act sequentially (Fig. 1). First, carbon from the above-ground litter layer reaches the mineral layer of the soil through the leaching of water-soluble organic carbon and through bioturbation by soil animals such as termites, earthworms, beetles, collembolans and woodlice.

The organic carbon leached from the litter then 'primes' soil microorganisms, which in turn accelerate the SOM turnover. Priming is a sequence of processes that increases the respiratory activity, enzyme production and total number of soil microorganisms, changing their community structure[7], and is based on interactions between living and dead organic matter[8]. It has been assumed that priming occurs in most plant–soil systems[6], but experimental evidence under field conditions and especially from long-term studies has been lacking. The study by Sayer and colleagues provides much needed evidence in support of that view[5].

Their study is not the first to look at the effects of doubled litter inputs on soil carbon. In contrast to previous studies, however, Sayer and colleagues used plant litter in which the isotopic signature was shifted so that changes in SOM cycling and decomposition could be traced over time. By changing the isotopic composition of the carbon input to the ecosystem, they monitored both the outputs and sources of the CO_2 and were consequently able to evaluate the changes to SOM cycling.

Their results show that the addition of plant litter to the soil resulted in priming that lasted for at least six years after the study began. They estimate that the CO_2 released through priming represents around 13% of total below-ground respiration. As litter input is expected to increase with primary productivity, this feedback is only likely to intensify in the future. Sayer *et al.* predict that a future increase in litterfall of 30% with a rise in atmospheric CO_2 concentration of 150 ppm could release around 0.6 tonnes of carbon per hectare per year from the soil (corresponding to 0.67% of total soil carbon stock in the upper 0–50 cm), an amount nearly equivalent to one cubic metre of petrol.

But faster decomposition of SOM under increased CO_2 concentrations does not necessarily lead to a decrease in the soil's carbon stock, as is frequently assumed. To investigate this, the balance between accelerated SOM decomposition

and increased carbon input from litter needs to be calculated. The lack of this particular calculation is one of the limitations of the study by Sayer and colleagues[5]. Another aspect that adds uncertainty to their predictions is the hidden assumption that litter produced under ambient CO_2, which is what they used in their study, would have the same effect on soil carbon as litter produced under increased CO_2 concentrations. Litter quality is one of the most important controls of terrestrial carbon storage[10]. Increased CO_2 concentrations generally lowers the quality — in particular the decomposability — of the litter because it then has a higher content of structural materials such as cellulose and lignin, which are difficult for microorganisms to break down. As a result, the effects of the activation of microorganisms arising from higher litter input may be counterbalanced by a decrease in litter quality.

The plant biomass that we see above-ground, which is what is considered in most global change studies, is only one part of the carbon assimilated from the atmosphere. The other part — frequently termed the hidden half — is located below-ground. This hidden half includes not only roots, but also mycorrhiza (fungi living in very close symbiosis with roots), as well as a broad range of organic substances released by roots and mycorrhiza that are known as rhizodeposits. Previous research[2] has shown that higher concentrations of atmospheric CO_2 increase below-ground plant biomass production and rhizodeposition even more than above-ground production (Fig. 1).

This means that below-ground inputs of root carbon under increased CO_2 concentrations will intensify the terrestrial carbon cycle even more than the effects of increased above-ground litter studied by Sayer and colleagues[5]. Consequently, it is necessary to look both above- and below-ground for a better understanding of the carbon cycle and prediction of the interactions that may counterbalance expected gains in carbon storage. ❑

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POLICY

Reconsidering Copenhagen

The voluntary emission reductions pledged under the Copenhagen Accord are almost certainly insufficient to limit global warming to 2 °C. However, using the Copenhagen Green Climate Fund for mitigation efforts could achieve the reductions needed to fill the gap.

Robert Marschinski and Michael Jakob

Never before has climate politics been more in the limelight than during the 2009 Copenhagen climate conference, when presidents and prime ministers gathered to find a successor agreement to the Kyoto Protocol. But the high expectations of many observers went unfulfilled, and criticism of a loose agreement based on voluntary targets was abounded. Most climate scientists doubted that an international policy following the 'collection-box principle'[1] — in which nations pledge to achieve voluntary goals — would achieve drastic emission cuts. Furthermore, they pointed out that even if all the pledges are achieved in full, temperatures will probably still rise by more than 3 °C (ref. 2). Writing in *Climatic Change*, economists Carlo Carraro and Emanuele Massetti[3] argue that this view might be overly pessimistic, because the Copenhagen Green Climate Fund (CGCF) — the second, and so-far less-appreciated, pillar of the Copenhagen Accord — could facilitate the additional reductions needed to avoid dangerous climate change.

With the approaching end of the first commitment period of the legally binding Kyoto Protocol, world leaders at Copenhagen were under pressure to establish a new agreement. Backed by an emerging consensus that the global average increase in temperature should be limited to 2 °C, and by evidence indicating that substantial emission cuts are needed in the near term to achieve this target, the debate focused on global reduction targets for the year 2020. Against this backdrop, the Copenhagen Accord was seen by most people as a huge disappointment, not only because of the shift from legally binding targets to 'pledges', but also because of the seemingly low level of emission reductions implied by the pledges.

Now Carraro and Massetti[3] challenge this position on three accounts. First, they argue that the focus on whether the envisaged 2020 emission reductions are in line with a 2 °C target is misleading, because global temperature change is determined by cumulative emissions over the entire twenty-first century. Second, the pledged reductions are far from insignificant. Third, taking only the pledges into account is also misleading, because the Copenhagen Accord consists of two intertwined pillars: reduction pledges and climate finance. A fair evaluation of the emission reductions that can be achieved by deploying climate funds must also be included.

The researchers started out by quantifying the emission reductions that the pledges could, in theory, achieve by 2020. Some countries offered to cut their emissions more drastically if other countries followed suit, so both 'high' and 'low' emission reductions scenarios were considered. Their analysis indicates that the pledges would reduce global emissions to 46.2 Gt of CO_2 equivalent (high reduction scenario) or 47.8 Gt of CO_2 equivalent (low reduction scenario), corresponding to a reduction of 14% and 11%, respectively,