organisms. Furthermore, it should encourage others to explore the use of mechanical signals to generate extra skin — not only for reconstructive surgery, but also for diseases associated with impaired regeneration.

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Biogeochemistry

Carbon loss from tropical soils increases on warming

Eric A. Davidson

Plots of tropical forest soils were warmed by 4 °C for two years to observe the effects on soil carbon emissions. The increase in efflux of carbon dioxide was larger than expected — a result with worrying implications for climate change. **See p.234**

The carbon stored in soil could have a big impact on climate change. The global flux of carbon in and out of soils is six to ten times greater than the emissions of carbon dioxide produced as a result of human activities[1,2]. The inputs of carbon to soils from plant detritus (dead wood, leaves and roots) roughly balance the losses to the atmosphere produced by the respiration of soil microorganisms that feed on that material. However, just a 1% imbalance of global soil-carbon effluxes over influxes would equal about 10% of global anthropogenic carbon emissions. Carbon in tropical soils was thought to be less vulnerable to loss under climate change than is soil carbon at higher latitudes, but experimental evidence for this was lacking. On page 234, Nottingham *et al.*[3] report that tropical-forest soils might be more vulnerable to warming than was thought.

Various soil management practices (such as changes of land use and of tillage methods) can influence the amount of soil carbon present[4], but climate affects the respiration rate of the microbes that feed on soil carbon, and hence the CO_2 efflux from soil[5]. If the net efflux of carbon from soils to the atmosphere increases in a warming world, a positive feedback will accelerate the warming.

Soils are amazingly diverse and differ in several respects that affect microbial respiration[6]. These include: the amount of minerals to which soil carbon can bind and thereby be protected from decomposition by microbial enzymes; water content, which affects the diffusion of carbon to microbial enzymes; the amount, timing and quality of the plant detritus going into the soil; and genetic variation in soil microbial communities. The intrinsic temperature sensitivity of microbial respiration reactions indicated by theory and demonstrated in the laboratory (where other factors are not limiting) therefore often varies from the apparent temperature sensitivity measured in real-world settings[5,6]. Several *in situ* soil-warming experiments have yielded insights into the effects of temperature on CO_2 efflux from soil in temperate and boreal regions[6,7], but such research is logistically more challenging to implement in tropical forests.

Nottingham and co-workers now present results of a soil-warming experiment (Fig. 1). The authors placed warming rods around the perimeter of undisturbed soil plots in a tropical forest on Barro Colorado Island, Panama, and increased the temperature of the whole soil profile (to a depth of 1.2 metres) by 4 °C for two years. They measured CO_2 efflux using chambers periodically placed over the soil, and observed an unexpectedly large increase (55%) in soil CO_2 emissions. By excluding roots from the soil under some of the chambers, the authors determined that most of the increased CO_2 efflux was due to a greater-than-expected increase in the respiration of soil microbes.

The dependence of reaction rates on temperature, including the rates of enzymatic reactions, is described by the Arrhenius equation[5]. According to this equation, the fractional increase in reaction rate is less for a temperature increase of one degree Celsius at higher temperatures than at lower temperatures. This suggests that the response of soil microbial respiration to temperature changes

Figure 1 | Preparing to use a heating device in an experiment. Nottingham *et al.*[3] buried heating equipment in plots in a topical forest in Panama and monitored the affect of warming on carbon dioxide release from the soil.

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should be less pronounced in tropical climates than it is in temperate or boreal climates. The Arrhenius relationship breaks down for enzymatic reactions at temperatures beyond those that are optimal for enzyme function, and therefore should not be extrapolated beyond temperatures that enzymes normally experience. But such extreme temperatures were not reached in Nottingham and colleagues' experiment.

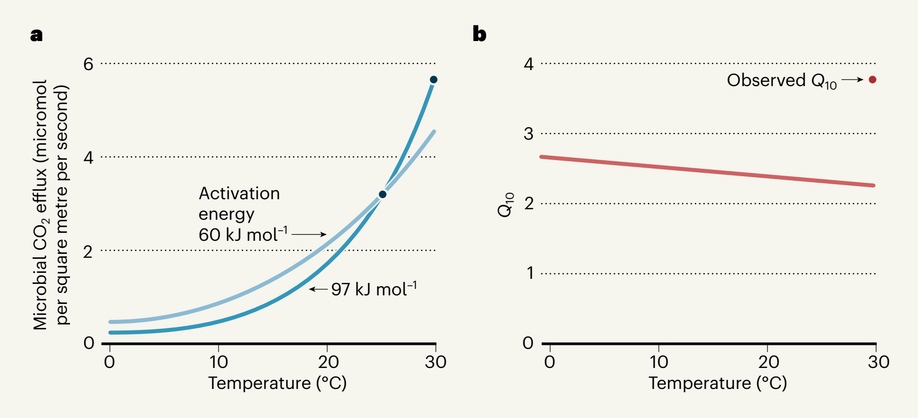

Figure 2 | Theoretical and observed temperature sensitivity of CO_2 efflux from tropical soils. **a**, Nottingham *et al.*[3] observed an increase in CO_2 efflux from tropical soils warmed *in situ* from an ambient temperature of 26 °C to 30 °C (dark blue circles). The pale blue line shows the theoretical dependence of CO_2 efflux associated with soil microbial respiration, calculated using an Arrhenius function[5] (which describes the kinetic response of enzymes to temperature) and assuming that the activation energy (E_a; simplistically, the minimum amount of energy needed for a reaction to occur) of the microbial respiratory reactions is 60 kilojoules per mol, which is typical for such reactions[8]. The observed increase in efflux on warming is larger than that predicted from this Arrhenius function. To fit the observations, E_a would have to be 97 kJ mol^{-1} (dark blue line), which is unlikely for respiratory enzymes. **b**, The Arrhenius function also predicts much lower Q_{10} values (red line; the multiplication factor of the increase in efflux observed when the temperature increases by 10 °C) than that observed by the authors at 30 °C (red circle). The authors' results suggest that unknown factors co-vary with temperature to increase CO_2 efflux, and that the kinetic responses of respiratory enzymes, alone, are insufficient to account for their observations.

Each enzyme-catalysed reaction has a characteristic activation energy (E_a, simplistically defined as the minimum energy needed for the reaction to occur), but the E_a values of the vast majority of respiratory enzymes fall within a fairly narrow range[8], averaging about 60 kilojoules per mol. If this common E_a value is used in an Arrhenius function to calculate how the average microbial CO_2 efflux from Nottingham and colleagues' plots varies with temperature (fitting the resulting curve to the efflux recorded in the non-warmed plots), the observed efflux from the warmed plots is found to be much higher than the calculated value (Fig. 2a). The E_a value would have to be an unlikely 97 kJ mol^{-1} to make the Arrhenius function fit with the efflux observed from the warmed plots.

A short-hand indicator of the temperature sensitivity of soil CO_2 efflux is Q_{10}, the multiplication factor of the increase observed when the temperature increases by 10 °C. The Q_{10} for microbial CO_2 efflux in Nottingham and co-workers' experiment was 3.6, which is well above expectations for most respiratory enzymatic processes on the basis of common E_a values and the Arrhenius equation (Fig. 2b). Temperature sensitivities as high as this indicate that the increased efflux in the warmed plots probably cannot be attributed only to the kinetic response of enzymes to warming – other confounding factors must also co-vary with temperature[9]. Indeed, in *in vitro* assays, Nottingham *et al.* report Q_{10} values of 2 or less for specific respiratory enzymes in soil samples from the studied plots. The authors rule out the possibility that significant confounding effects arose during their warming experiment as a result of the modest changes in soil-water content and microbial carbon-use efficiency. The cause of the unexpectedly high observed apparent temperature sensitivity therefore remains a mystery.

These results suggest that caution is needed when using only an Arrhenius or Q_{10} function to describe the temperature responses of soil microbial respiration – which most numerical models of Earth's systems and their carbon cycling responses to climate change unfortunately do[10]. The Arrhenius function (where E_a is about 60 kJ mol^{-1}) predicts a modest decrease in Q_{10} from about 2.6 at temperatures typical of high-latitude ecosystems to 2.2 at temperatures typical of tropical forests (Fig. 2b), whereas the current study and others[2,5,6] report a broader range of observed Q_{10} values.

Nottingham and colleagues' results suggest that other factors affecting soil CO_2 efflux merit further study. Efflux responses to experimental warming often decline after a few years, perhaps because the readily decomposable components of soil carbon that act as substrates for respiration reactions become depleted, or because of shifts in microbial community structures[6,7]. The Panamanian forest soil studied in the present work is relatively fertile as a result of the historical deposition of volcanic ash; this soil fertility might have enabled high rates of inputs of plant detritus to the soil, preventing soil microbial respiration from being limited by the availability of substrates. Indeed, the authors report an increase in soil microbial biomass in the warmed plots compared with control plots, indicating that warming might have increased the total microbial enzymatic capacity – thereby increasing CO_2 efflux beyond the expected kinetic response of the pre-existing enzymatic capacity.

> **"Tropical forests are unlikely to continue indefinitely to be carbon sinks as the world warms."**

Besides the clear take-home message that the responses of soil respiration processes under climate change should not be represented in Earth-system models only by simple Q_{10} or Arrhenius functions, Nottingham and co-workers' study adds to recently accumulating evidence that tropical forests are unlikely to continue indefinitely to be carbon sinks as the world warms[11]. Tropical soil carbon does not receive as much attention as do the large and vulnerable soil-carbon stocks at high latitudes, which pose major concerns as a potential source of positive feedback to climate change[12]. But tropical-forest soils also contain substantial carbon stores that might be more vulnerable to loss in a warming world than was previously recognized.

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