

Hsieh and Jewitt believe that the likely answer for main-belt comets is that they have suffered a small collision in the recent past, which has exposed subsurface ices to solar heating, and that these ices may sublimate on and off for at least several years before exhaustion. This is supported by observations showing that 133P/Elst-Pizarro has been only sporadically active over the past decade (9, 10). Given that last year's spectacular Deep Impact mission (11) did not result in a new activity site on a normal Jupiter-family comet, our demonstrable lack of knowledge of how sublimation sites are activated implies that a better estimate of the sublimation lifetime is unlikely in the near future.

It is also unclear how many main-belt comets may exist. Hsieh and Jewitt estimate that there may be as many as 150 currently detectable in this new population, although they caution that true numbers will require a much larger systematic survey. The excitement for planetary scientists is that we now have a new direction in which to study the composition of the solar system. Current

theories predict that both Jupiter-family comets and long-period comets formed in the outer solar system beyond Jupiter and were scattered into their present orbits via various gravitational perturbations. The main-belt comets are relatively immune to such effects and should be pretty close to their birthplace. Hence, by studying the ices in these comets, astronomers could look for changes in the ice composition in the protoplanetary disk. This makes main-belt comets a prime target for future space missions, but it may be possible to start such studies using the next generation of optical, infrared, and submillimeter telescopes currently being built or planned.

At the same time, Hsieh and Jewitt note that the outer asteroid belt has been proposed as a source of the water deposited on Earth after the end of the planet-building phase. This work should spur a closer assessment of recent dynamical models predicting delivery of large numbers of objects from this region into near-Earth space (12). It is interesting that many astronomers have pursued comets to greater and greater distances

in their pursuit of understanding the evolution of comets and the early history of the solar system. All this time, it would have also been worthwhile to look a little closer to home.

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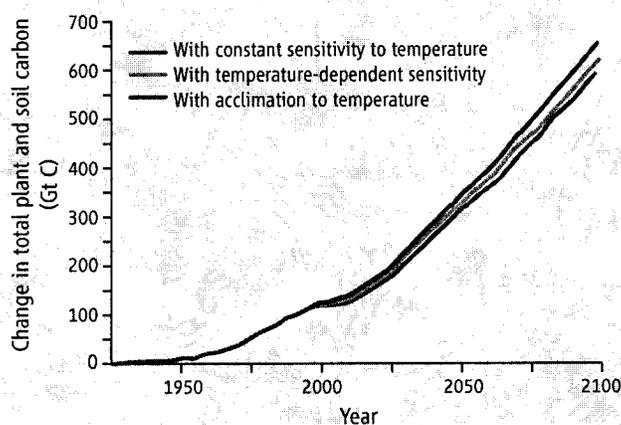
ATMOSPHERE

Plant Respiration in a Warmer World

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Plants release carbon dioxide as they metabolize carbon substrates for biosynthesis and maintenance of the biochemical machinery of life (1, 2). This respiratory process globally transfers about 60 gigatons of carbon each year to the atmosphere (3). It has been predicted that plant respiration, and leaf respiration in particular, will increase in a future warmer world. But are these predictions consistent with observations from modern experimental studies?

Numerous studies have shown that respiration increases in response to an increase in temperature (4, 5). Higher plant respiration at warmer global temperatures would release more CO₂ to the atmosphere, resulting in lower net ecosystem carbon uptake, even higher atmospheric CO₂ concentrations, and consequently more warming. Incorporating biotic feedbacks like this in coupled climate-carbon models results in an additional increase of



The effect of respiration. Cumulative change in global total terrestrial biosphere carbon simulated by the GTEC 2.0 model, using different temperature dependencies for leaf maintenance respiration. See supplementary online material.

simulated mean annual land-surface temperatures of as much as 2.5°C by 2100 (6, 7).

However, many studies have shown that the increase in plant respiration in response to an increase in temperature is a short-term, largely transient response that is observed when plants grown at a controlled temperature are experimentally exposed to warmer temperatures. In the longer term, plant respiration may acclimate to

warmer temperatures. Plant respiration is likely to contribute to positive feedbacks in global warming, but acclimation of plants to higher temperatures may reduce the extra warming caused by increased respiration in a warmer world.

warmer temperatures. Plants experimentally grown at higher temperatures often respire at nearly the same rate as plants grown at cooler temperatures, even though a short-term warming of either set of plants would produce a typical exponential response to temperature (8-10). In addition, plants from warmer climates often show a much-reduced sensitivity to temperature change when compared to plants from cooler climatic regions (11). The biochemical basis for acclimation is not yet known. Mechanistic synthesis, understanding, and modeling are thus problematic, and a mechanistic representation of the acclimation of plant respiration to temperature is

generally absent from climate change analyses and carbon cycle models. An increasing number of physiological studies do, however, support the conclusion that the long-term response of respiration to temperature may be quite different from the more commonly measured and short-term response.

Acclimation of respiration to elevated temperatures has clear implications for predictions

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and expectations of higher plant respiration in a warmer world. For example, reduced sensitivity of respiration to temperature increase could reduce the magnitude of the positive feedback between climate and the carbon cycle in a warming world. Yet, though most coupled climate-carbon models include an increase in leaf and plant respiration in response to elevated temperature, none in the C⁴MIP climate-carbon model inter-comparison (12) and no others to our knowledge include an explicit time-dependent acclimation of plant respiration to increasing temperatures. Some differentiate among vegetation types, such that the response to warming temperatures of tropical vegetation is smaller than that of boreal vegetation, for example. And in some, the sensitivity to temperature depends on temperature, so that respiration increases more slowly with warming at higher temperatures than at cooler temperatures. But even these models do not include the time-dependent acclimation to a change in temperature within a few days observed in experiments (9).

Recent work with an ecosystem-scale model showed how acclimation of respiration to changing temperature could have a substantial effect on rates of aboveground net primary production (13). To explore this issue further, we have investigated the influence of temperature acclimation of leaf respiration on simulated carbon dynamics and climate-carbon feedbacks at both the local ecosystem scale and the global scale. Plant parts other than leaves are also likely to acclimate to warmer temperatures, but because more is known about leaves, we have limited our analysis to leaf respiration.

The figure compares the changes from 1930 to 2100 of total carbon stored globally in plants and soils simulated by a global terrestrial ecosystem model, GTEC 2.0 (14), with and without acclimation of leaf respiration. The standard version of the model uses a constant sensitivity to temperature; the sensitivity to temperature varies with vegetation type, but does not change with time or temperature. As did Wythers et al. (13) in their ecosystem-scale model, we performed two further model runs but at the global scale, one with a temperature-dependent sensitivity to temperature (the increase in respiration with increase in temperature is less at warmer temperature, and respiration actually declines with even further warming) and one with an empirical representation of the acclimation of leaf respiration to temperature change based on observations from plant-warming experiments (14).

The simulated increase in total carbon stored globally in plants and soil is smallest with the constant sensitivity to temperature, slightly higher with temperature-dependent sensitivity, and largest with acclimation (see the figure). With acclimation (even the partial acclimation we model), leaf respiration at the higher temperatures at the end of the 21st century is reduced, and more carbon is stored in plants and soils. All other

things being equal, as they are in our simulations, more carbon stored in plants and soils corresponds to less carbon released to the atmosphere in response to climate change, and a weaker positive feedback between carbon and climate and a weaker amplification of additional warming.

Thus, acclimation of leaf respiration (a known phenomenon, but one not normally included in coupled climate-carbon models) has the potential to reduce the strength of the positive feedback between climate and carbon commonly found in coupled climate-carbon simulations. The effect in the reported simulations is small compared with differences among models (12), and our sensitivity analysis (14) uses a single empirical representation of leaf acclimation drawn from a limited set of experiments. Nevertheless, the influence of acclimation of leaf respiration to temperature is of sufficient magnitude in our analysis to suggest that it should be incorporated into plant, ecosystem, and coupled climate-carbon simulations.

There is also a need to better understand the control of respiration itself. The development, testing, and adoption of a mechanistic and biochemical model of plant respiration are needed. To more reliably project plant respiration and climate-carbon feedbacks in a future climate, this modeling must incorporate response to temperature, including acclimation, at time scales from minutes to years.

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14. For further details on the model runs see the supplementary online material.

Supporting Online Material

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SOM Text

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EVOLUTION

Size Does Not Matter for Mitochondrial DNA

Adam Eyre-Walker

That large populations harbor more genetic diversity than small ones holds true for nuclear genomes, but may not apply to mitochondrial DNA. If so, the use of mitochondrial DNA as a standard for genetic diversity may not be wise.

On page XXX of this issue, Bazin et al. test one of the most basic predictions of population genetics: that species with large population sizes should have more genetic diversity than species with small population sizes. They find that this prediction, as expected, is upheld for diversity in nuclear genes, but that there is no correspondence between population size and genetic diversity for mitochondrial genes.

Bazin et al. conducted their analysis by first compiling an impressive DNA diversity

data set for both nuclear and mitochondrial DNA. Using an automated system, they searched the GenBank and EMBL databases for instances in which the same gene had been sequenced in multiple individuals of a species. This yielded, after some restrictions to improve data quality, 417 species for which they had diversity data for nuclear DNA and 1683 species for mitochondrial DNA. They also analyzed a data set of 912 species for which allozyme diversity data were available.

Unfortunately, the census population size is not known for the vast majority of organisms, so Bazin and colleagues used a number of phylogenetic and ecological factors to test whether population size and diversity were correlated. For example, they tested whether invertebrates

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