the view that we are directly seeing the "epicyclic" periods general relativity predicts for the orbital motion of test particles: one related to the well-known general-relativistic precession of Mercury's orbit (but 10^{17} times faster because of the strong gravity) and another to the so-called "Lense-Thirring precession" of the orbital plane itself, caused by "frame-dragging," a phenomenon in which a spinning object drags space-time around it along with its spin (*9*). But there seems to be more to it than that. RXTE has discovered the first millisecond pulsar in an x-ray binary, a neutron star spinning with a 2.493919753-ms period (*10*), and has measured the approximate spins of another six neutron stars with periods of 2 to 4 ms (*11*). Comparison of these spins with the millisecond quasi-periods suggests that while the fastest of the two quasi-periods seen in each system originates in the orbital motion in the accretion disk, the slower one (still sometimes as fast as 1.2 msec) arises by a nonlinear interaction (a "beat") between the spin and the orbital motion. One model describes a pattern of orbital motion that could explain the observations in detail (*7*). A few more years of observations, more discoveries, and further high-precision measurements of the new phenomena will show which of these theories can be maintained and which must be abandoned.

RXTE's success has demonstrated that when probing the dynamics in strongly curved space-time, there is no substitute for size. It is the huge effective area of 0.7 m^2 of the main x-ray instrument onboard the satellite that gave Rossi the sensitivity to make the first direct measurements of orbital motion near collapsed stars. To fully exploit these discoveries and map out space-time near neutron stars and black holes, an instrument in the 10-m^2 class will be required. Although the stream of new data from RXTE continues unabated and a second millisecond timing mission (the Naval Research Laboratory's Unconventional Stellar Aspect experiment on the Argos satellite) was just launched successfully, x-ray astronomers are already considering the new solid-state technologies by which such a "relativity explorer" might be realized.

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PERSPECTIVES: PALEOECOLOGY

Plants and Temperature-CO_2 Uncoupling

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Measurements of CO_2 and oxygen isotopes in polar ice caps indicate that for at least the past 420,000 years, temperature and CO_2 trends have been coupled; cooling generally coincides with low CO_2 and warming with higher CO_2 (*1*). This observation may lead us to believe that changes in CO_2 and temperature have been coupled throughout Earth's history and will continue to be coupled in the future. However, recent estimates (*2–4*) of CO_2 concentrations of 180 to 240 μmol mol^{-1} for the mid-Cenozoic [between 17 and 43 million years ago (Ma)] are well below modern CO_2 concentration of 360 μmol mol^{-1}, at a time when at least some regions are thought to have been up to 6°C warmer than today (*5*). Degassing of biogenic methane hydrates may have been responsible for abrupt mid-Cenozoic warming (*6*); however, increases in other greenhouse gases such as water may have also caused temperatures to rise without concurrent increases in atmospheric CO_2. Such temperature-CO_2 uncoupling, if confirmed by further studies, may influence our ideas about climate-forcing mechanisms (*5*) and paleoecosystem form and function.

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Temperature-CO_2 uncoupling is predicted to have strong effects on the fundamental process of carbon fixation in most plants. There are two major classes of plants defined by their carbon fixation pathway—C_3 and C_4. The primary enzyme for carbon fixation in C_3 plants—mostly tropical grasses—is ribulose-1,5-bisphosphate (or Rubisco). Rubisco fixes O_2 in competition with CO_2 in a process called photorespiration, which results in a loss of fixed carbon and reduced efficiency of C_3 photosynthesis. Reductions in atmospheric CO_2 and rises in temperature independently increase photorespiration (*7*). In a scenario where climate-CO_2 trends are uncoupled so that climate warming is not accompanied by increases in atmospheric CO_2, C_3 photosynthesis may be extremely low because of high rates of photorespiration. In contrast, because the primary carboxylating enzyme in C_4 plants does not react with O_2, C_4 plants can out-compete C_3 in low CO_2 and high temperature environments (*8*).

Our present understanding of how C_3 plants respond to changes in temperature and CO_2 can be used to constrain low-end CO_2 estimates made from geological data, particularly for the Cenozoic before 15 Ma, when terrestial ecosystems predominantly contained plants with the C_3 photosynthetic pathway. Because the paleorecord indicates that land plants survived and thrived throughout the Cenozoic, any geologically predicted CO_2-

TEMPERATURE–CO_2 INTERACTIONS AND PLANT CARBON

Experiment	CO_2 (μmol/mol)	Temperature (°C)	Photorespiration* (percent)	Net photosynthesis (μmol/m^2s)
Modern	360	25	11	17
control	360	32	18	11
LGM†	200	25 – 5	15	10
	200	32 – 5	24	8
Miocene‡	260	25 + 2	18	11
	260	25 + 5	22	9
	260	32 + 2	29	6
	260	32 + 5	35	4
	220	25 + 2	21	9
	220	25 + 5	26	7
	220	32 + 2	34	4
	220	32 + 5	41	3
Eocene§	385	25 + 2	12	16
	385	25 + 5	15	14
	385	25 + 2	19	10
	385	32 + 5	24	7
	180	25 + 2	26	7
	180	25 + 5	32	5
	180	32 + 2	41	3
	180	32 + 5	50	1

* Percent of gross photosynthesis. † Last Glacial Maximum (LGM, 21,000 years ago). ‡ Miocene CO_2 limits from (*2*). § Eocene CO_2 limits from (*3*).

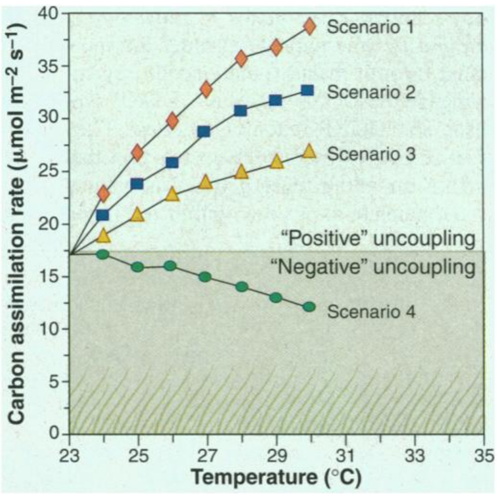
temperature combination that promotes extremely low plant carbon (that is, very high photorespiration) may be unlikely from a biological perspective.

Low-end mid-Cenozoic CO_2 estimates provided by Pagani *et al.* [220 μmol mol^{-1} (*2*)] and Pearson and Palmer [180 μmol mol^{-1} (*3*)] can be assessed physiologically with photosynthetic modeling experiments (*9, 10*). The magnitude and spatial extent of mid-Cenozoic warming remain uncertain, and therefore conservative (2°C) and high (5°C) climate warming scenarios have been considered here (*11*).

Low-end CO_2 estimates of 220 μmol mol^{-1} (*2*) and below (*3*) are not biologically supported because simulated photorespiration rates in low latitudes under minimal 2°C warming are over 30% of gross photosynthesis, with carbon assimilation rates as low as 4 μmol m^{-2} s^{-1} and below (see the table). The same conclusion can be drawn from low- and mid-latitude data under simulated extreme (5°C) climate warming (see the table). Carbon-limiting environmental stresses such as drought, nutrient limitations, plant-plant competition, and herbivory may also have been present, depressing plant carbon balance even further. It therefore seems very unlikely that mid-Cenozoic atmospheric CO_2 could have dropped to 220 μmol mol^{-1} and below.

The upper CO_2 limit predicted for the Eocene (around 43 Ma) by Pearson and Palmer (*3*) results in modeled photosynthetic rates that are reasonably close to modern-day controls (see the table). However, the upper CO_2 limit predicted for the Miocene (around 17 Ma) by Pagani *et al.* (*2*) may, or may not, be plausible from a biological perspective. Because climate and CO_2 at the Last Glacial Maximum resulted in substantial vegetation changes arising from altered plant carbon and water balance (*12*), then the lower photosynthetic rates simulated under predicted Miocene CO_2 concentrations of 260 μmol mol^{-1} (*2*) (see the table) indicate that similar, or even greater, changes to global vegetation patterns should have occurred.

The paleorecord may already contain such a signal, suggesting that a low-end CO_2 estimate of 260 μmol mol^{-1} for 17 Ma (*2*) may not be so biologically unreasonable. Although some data indicate evolution of the C_4 photosynthetic pathway before the Miocene (*13*), evidence of widespread presence of C_4 photosynthesis dates from about 15.5 Ma onward (*14*). Stable carbon isotope data from fossil herbivore teeth indicate a substantial expansion of C_4-dominated grasslands in tropical Asia, North America, South America, and Africa between 7 and 5 Ma (*15*). Theories on the environmental conditions that could have facilitated C_4 plant evolution include mid-Cenozoic reductions in CO_2 below a threshold of 500 μmol mol^{-1} (*16*) and increased Miocene aridity (*17*). Climate-CO_2 uncoupling, however, could play a more direct role in the selection and propagation of C_4 traits in land plants because such events would have resulted in even greater carbon and moisture stress (through high photorespiratory carbon losses) than low CO_2 alone, thus heightening plant susceptibility to increased aridity. The effects of temperature-CO_2 uncoupling on plant-carbon balance may also explain why Eocene rates of herbivory seem to have been higher than during the Paleocene (*18*), a period for which CO_2-temperature uncoupling events have yet to be identified. Low carbon assimilation rates could have led to a reduction in the production of secondary carbohydrates such as phenols and other herbivore-defense compounds, rendering Eocene leaves more palatable for herbivores than Paleocene leaves.



Photosynthetic response to potential future temperature-CO2 scenarios. The solid line illustrates a perfectly coupled CO_2-temperature increase scenario, where assimilation remains about constant with increasing temperature. Curves above this reference line are termed "positive uncoupling" because temperature increases lag CO_2 increases, allowing assimilation rates to increase with rising temperature. Curves below the reference line are termed "negative uncoupling" because temperature increases surpass those in atmospheric CO_2, with assimilation rates decreasing with higher temperatures. Scenario 4 represents temperature increases at constant CO_2 (360 μmol mol^{-1}). All CO_2 increase scenarios were started at CO_2 concentrations of 360 μmol mol^{-1}.

Understanding the role of temperature-CO_2 uncoupling for past ecosystems is important for predicting future vegetation-climate interactions. If temperatures rise by 1°C for every 227 (scenario 1), 136 (scenario 2) and 76 μmol mol^{-1} (scenario 3) increase in atmospheric CO_2 (*19*), assimilation rates will continue to rise, indicating the absence of negative uncoupling effects on plant carbon (see the figure). In all three scenarios, C_3 plants will be able to respond to increases in atmospheric CO_2 without having to allocate excessive energy and essential plant nutrients for biochemical adjustments to higher growth tempertures (see the figure), reconfirming similar conclusions made by Long (*20*) nearly a decade ago. But maybe we should be less concerned about rising CO_2 and rising temperatures and more worried about the possibility that future atmospheric CO_2 will suddenly stop increasing, while global temperatures continue rising.

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