PERSPECTIVES: PALEOCLIMATE

Kilimanjaro's Secrets Revealed

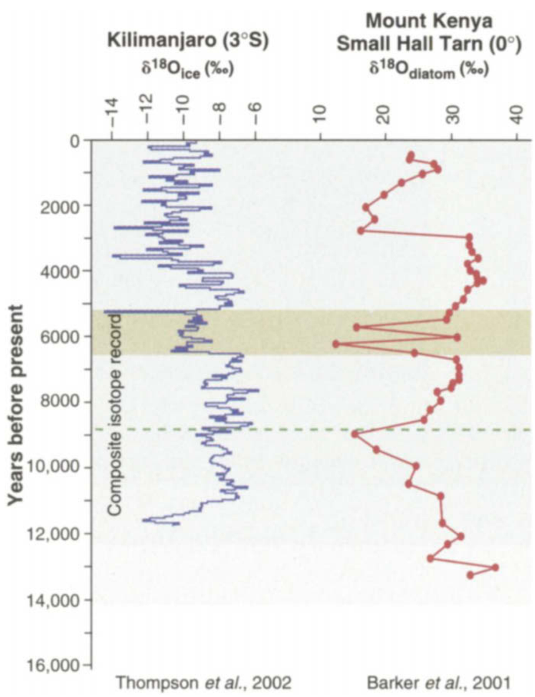
Françoise Gasse

Tropical climate fluctuates on various time scales, from interannual (exemplified by the strong 1997–1998 El Niño) to thousands of years (such as the greening of the Sahara from ~10,000 to ~5500 years ago) (*1*). At present, 75% of the world's inhabitants live in the tropics. Low-latitude climate fluctuations thus have a considerable societal impact. Because instrumental records are short, paleoclimate records are essential to understanding the full range of tropical climate variability, its effects on Earth's energy budget and water vapor cycle, the connections between high- and low-latitude climate, and the sensitivity of the tropics to future climate change.

On page 589 of this issue, Thompson *et al.* (*2*) present the first ice core record from Africa. The record complements ice core evidence for tropical climate change from other continents (*3*). The new record comes from Kilimanjaro, Africa's highest peak, which lies near the equator in the East African monsoon region. The nearly continuous, high-resolution record spans the entire Holocene from ~11,500 years ago to the present. The authors infer temperature fluctuations from changes in the ice oxygen isotope ratio, $\delta^{18}O$. They use high concentrations of insoluble dust and major aerosol species as fingerprints of large-scale drying trends, and peaks in F^- and Na^+ as possible indicators of more local erosion during strong but brief drying events.

At the millennial time scale, Thompson *et al.* (*2*) distinguish two climate phases: conditions warmer and wetter than today from ~11,000 to ~4000 years ago, and a relatively dry and cool climate over the past ~4000 years. This pattern agrees with numerous continental and marine records showing that the monsoon circulation and related rainfall over the northern tropics and equatorial East Africa were considerably stronger during the early to mid-Holocene as a result of changes of Earth's orbit around the Sun (*1, 4*).

Superimposed on these general trends are abrupt events on time scales of decades or centuries that strongly affect human societies. Understanding these short-term variations requires accurate and well-dated records. Unfortunately, dating tropical ice cores is a difficult exercise. The depth-age model used by Thompson *et al.* (*2*) does not provide an absolute chronology. The small amount of organic material does not yield consistent ^{14}C ages. The authors assign ages to three ice layers. The 1952 layer is identified accurately on the basis of a ^{36}Cl peak from a thermonuclear bomb test. The age



The climate in Africa. Oxygen isotope records from neighboring high-altitude sites in tropical Africa. The Kilimanjaro record (*2*) is a composite record from three ice cores. The second record comes from an alpine lake on Mount Kenya (*14*). Marked $\delta^{18}O$ depletions, for example, from ~6500 to ~5200 years ago, are interpreted as reflecting a substantial cooling (*2*) or heavy convective precipitation (*14*).

for the core base derives from comparison with an Eastern Mediterranean speleothem. The third age is based on assumed relationships between $\delta^{18}O$ minima and solar activity minima in the upper part of the sequence.

These correlations are questionable and the precise timing of climate events proposed by the authors should be regarded with caution. Nonetheless, the reliability of the Kilimanjaro ice core chronology seems to be supported by its coherence with the timing of prominent known events.

Thompson *et al.* (*2*) suggest a substantial cooling in equatorial Africa during the Little Ice Age (from ~1270 to 1850), a cold spell in Europe and many other parts of the world (*3, 5, 6*). This large-scale event led to different hydrological responses over East Africa and the western Indian Ocean. Lake Malawi, in the southern East African tropics, experienced a period of low water level (*5*). In contrast, the Lake Naivasha basin in Kenya was relatively wet (*7*), especially during the Maunder Minimum of solar activity, when a minimum in monsoon strength occurred in the Arabian Sea (*8*). This illustrates the complexity of Little Ice Age climate variability in the region.

The authors add new evidence for three major dry spells at ~4000, ~5200, and ~8300 years before the present, already identified at some sites in the northern monsoon domain and related to large-scale events (*1, 4, 9*). A drought ~4000 years ago, linked to societal disturbances in Egypt, Mesopotamia, and India, has been identified in the Middle East and North Africa (*4*) and associated with a cooling in the North Atlantic (*10*).

The rapid drying and cooling event ~5200 years ago falls within the abrupt termination of the "African humid period" in the northern tropics. This event can be explained by feedback processes associated with changes in sea surface temperature and vegetation cover, which amplified the climate response to gradual changes in solar radiation received at the top of Earth's atmosphere (*11*).

The tropical drought at 8300 years before the present corresponds to a brief cooling in northern high latitudes and a global reduction in the atmospheric methane concentration (*5*). An oxygen isotope study of a stalagmite from Oman, where high $\delta^{18}O$ values are ascribed to reduced monsoon rainfall intensity, suggests that this centennial decrease in tropical precipitation was primarily controlled by changes in solar activity. These changes likely induced changes in atmospheric or ocean circulation that amplified the response to solar input change (*9*).

Thompson *et al.* (*2*) assume a positive relation between $\delta^{18}O$ and air temperature, and thus they interpret a marked $\delta^{18}O$ depletion from 6500 to 5200 years ago as a substantial cooling. A mid-Holocene cooling-wetting in equatorial East Africa has been suggested from glacier advance, pollen, and lake sediment records (*12*).

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But important questions arise from the short-term $\delta^{18}O$-inferred temperature fluctuations at Kilimanjaro. In the tropics, the $\delta^{18}O$ values of rainfall exhibit a far stronger correlation with rainfall amount than with air temperature (*13*). The few detailed lake and stalagmite oxygen isotope records available in the East African–South Asian monsoon domain (*9, 14, 15*) have thus served as a proxy for variations in monsoon rainfall.

Recently, a postglacial oxygen record from diatom silica in some alpine lakes at Mount Kenya, supported by a well-constrained ^{14}C chronology (*15*), was interpreted by considering the factors governing the regional isotopic rainfall composition. The authors (*15*) concluded that centennial- to millennial-scale $\delta^{18}O$ fluctuations primarily reflect variations in moisture balance and cloud height driven by sea surface temperature anomalies over the tropical South Indian Ocean.

The Mount Kenya and Kilimanjaro isotope profiles show similarities (see the figure), but the marked $\delta^{18}O$ depletions at ~6500 to 5200 years before the present were interpreted differently: Barker *et al.* argue that they reflect anomalously heavy snowfall (*15*), while Thompson *et al.* interpret them in terms of a substantial cooling (*2*).

The relative roles of temperature, water vapor trajectory, and precipitation amount on the tropical-montane isotope records thus remain controversial (*15*). Improving the global network for isotopic composition of precipitation (GNIP) (*16*) should resolve this question by helping to calibrate the tropical rainfall $\delta^{18}O$ composition in terms of climate parameters.

The unique ice core record of African climate presented by Thompson *et al.* (*2*) is also probably the last. The Kilimanjaro ice fields are shrinking fast in response to global warming, as are other tropical glaciers (*3, 13*). If the climatic trends of the 20th century continue, the ice on Kilimanjaro will disappear in the next 15 to 20 years (*2*). In the tropics, human societies suffer more from declining or irregular water resources than from changes in temperature. But global warming may have serious implications for local populations that depend on glacier meltwaters for farming, irrigation, or hydroelectric power. There is also an urgent need to collect high-quality cores from tropical glaciers that will not preserve paleoclimatic archives for much longer.

References and Notes

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PERSPECTIVES: MOLECULAR BIOLOGY

New Proteases in a Ubiquitin Stew

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Some people like to say that they can tell the type of person you are by the company you keep. Many biologists regard this bromide as an effective guide to understanding intracellular proteins as well. Certain intracellular proteins are only active when built into larger protein complexes that coordinate multiple biochemical activities. The interactions between proteins in these complexes are frequently regulated in response to environmental stimuli or to changes in cell state, such as passage through the cell cycle. This regulation is most often mediated by reversible attachment of chemical modifiers, such as phosphate or acetyl groups. Polypeptides such as ubiquitin can also reversibly modify other proteins. Ubiquitin and ubiquitin-like proteins (Ubls) are enzymatically ligated to lysine side chains of protein substrates, forming amide (isopeptide) bonds. When attached as either monomers or polymers, ubiquitin modifiers promote or inhibit binding of the modified protein to specific targets. Binding of polyubiquitinated proteins to the proteasome results in adenosine triphosphate (ATP)–dependent proteolysis of the protein substrate, with recovery of the intact ubiquitin tag.

Two studies—by Verma *et al.* (*1*) on page 611 of this issue and by Yao and Cohen in *Nature* (*2*)—demonstrate tight coupling between degradation and deubiquitination of protein substrates in the proteasome. Inactivation of the deubiquitinating enzyme (DUB) that releases ubiquitin chains from the proteasome completely prevents protein substrate degradation (*1*). Unexpectedly, the data suggest that the DUB is a proteasome subunit (Rpn11 or POH1) and may be a metalloprotease. The predicted protease motif, described in these papers and in an accompanying report by Cope *et al.* (*3*) on page 608 of this issue, has a widespread distribution in proteins from bacteria to mammals.

Cope *et al.* (*3*) analyzed an Rpn11-related protein, Csn5, which is part of another protein complex, the COP9-signalosome (CSN) (*4*). The CSN is an eight-subunit heteromultimer similar in sequence and organization to a subparticle of the proteasome termed the "lid" (see the figure). Both Csn5 and the Rpn11 lid subunit must be incorporated into larger complexes before they are activated. Last year, the CSN was shown to promote the removal of a Ubl known as Rub1 or Nedd8 (here referred to as Rub) from a subunit of the SCF ubiquitin ligase, which is crucial for cell cycle progression (see the figure, A) (*5*). What had been puzzling about the earlier CSN study (*5*) was that every DUB and Ubl-cleaving enzyme identified in prior work had proved to be a cysteine protease. Yet no cysteine residue in any CSN subunit is both evolutionarily conserved and sensitive to mutation. In the new work, Cope *et al.* detect a His-X-His-X_{10}-Asp motif (the JAMM motif) in Csn5. The conserved amino acids in this sequence often coordinate metal ions in the active sites of hydrolytic enzymes. Cope *et al.* hypothesized that a Rub isopeptidase active site in the CSN is formed by this motif (together with a potentially important Glu residue further upstream). Subsequent biochemical and genetic experiments indicated that this motif is likely to be a metal-binding site necessary for cleavage of Rub from SCF.

Much more is known about the biochemical activities of the proteasome than of the CSN. The proteasome is a proteolytic machine that recognizes polyubiquitinated protein substrates, unfolds them, threads them

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