tease for degradation (see the figure). The ribosome thus acts as a "starvation sensor," signaling through ppGpp to the cell that it needs to tap into amino acid reserves.

How are ribosomal proteins made available for degradation? Kuroda *et al.* found that polyphosphate does not destabilize intact ribosomes, although they did not rule out other factors causing ribosomal disassembly during a nutritional downshift. If ribosomes are not disassembled during a downshift, then the usual regulation of ribosomal protein synthesis and assembly must be sufficiently flexible in rapidly growing cells to ensure that a store of accessible amino acids (in the form of free ribosomal proteins) is always available. Even if polyphosphate-dependent degradation is not restricted to ribosomal proteins, the increase in protein turnover during the transition phase following a nutritional downshift may be more selective than previously thought.

The adaptation of cells to a decrease in amino acid availability may differ from long-term adaptation to true starvation—in the signaling molecules used, the proteins degraded, and the proteases involved. Cells deprived of essential elements such as carbon, nitrogen, sulfur, phosphate, or metal ions, or permanently deprived of an amino acid through mutation of its biosynthetic enzyme, must enter a holding phase during which no increase in cell mass is possible. In contrast, cells undergoing a nutritional downshift need only readjust their metabolism to begin exploiting less-efficient sources of essential nutrients. It remains to be seen whether other sacrificial substrates degraded under starvation conditions are targeted by polyphosphate.

In eukaryotes, proteins to be degraded are first bound to ubiquitin, a delivery tag that targets the substrate to 26*S* proteasomes or to lysosomes for degradation. Selection of substrates for ubiquitination is under the control of a panoply of ubiquitin protein ligases, each associated with adaptor proteins. These adaptors recruit different families of proteins to the ligase depending on the presence of specific binding motifs (*6*). Although ubiquitin tagging is absent in prokaryotes, other adaptor proteins have evolved alternative ways to recruit specific proteins to any of five known ATP-dependent proteases. For example, phosphorylation of a response regulator that interacts with both the sigma factor RpoS and the ClpXP protease results in degradation of RpoS (*7*); degradation of SsrA-tagged proteins by ClpXP is accelerated by yet another adaptor, SspB (*8*).

Polyphosphate is particularly suitable as an adaptor during nutritional downshifts because its synthesis does not require amino acids. How does polyphosphate promote protein degradation? Perhaps the proximity of protein substrate and protease is sufficient to allow capture and degradation of the bound protein. Alternatively, the Lon protease may recognize a motif on the bound protein or some other region that becomes exposed once the protein interacts with polyphosphate.

Polyphosphate is found in all cells, including those of mammals. As it also accumulates when cells are under nonnutrient stress, its interactions with certain target proteins may turn out to be unrelated to protein degradation. The Kuroda *et al.* work should spur new investigations into this ubiquitous polymer and its importance in protein degradation and other stress responses.

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PERSPECTIVES: VOLCANOLOGY

Predicting Volcanic Eruptions

Roberto Scarpa

In the past decade, some major explosive volcanic eruptions have been forecast successfully, for example, at Pinatubo, Philippines, in 1991, Rabaul, New Guinea, in 1994, and Soufriere Hills, Montserrat, in 1995. Anomalous geophysical signals were correctly interpreted as early warnings of an impending eruption, and cities at the foot of these volcanoes were evacuated several hours to weeks before the renewal of explosive activity. Nevertheless, volcanic eruptions and their secondary effects, such as lahars or mudflows, still claim many lives, for example, in the eruptions of Nevado del Ruiz, Colombia, in 1985 and Lake Nyos, Cameroon, in 1986, both of which caused thousands of deaths.

The reason for this discrepancy is that no rigorous methodology exists for predicting an impending eruption and the evolution of eruptive activity. Early detection of volcanic activity is mainly based on the observation of an anomalous increase in seismic activity and ground deformations. Substantial variations in these factors, which are a result of increased pressure of the magmatic system and magma motion, certainly constitute a basic tool for issuing a warning (*1*), but not all volcanoes behave as expected, and existing data are too limited for reliable prediction on a global scale.

That may soon change. In the past two decades, the temporal and spatial resolution of ground deformation data has increased rapidly through use of the Global Positioning System (GPS) and satellite radar interferometry. In addition, seismological observations now provide information about the underground structure and the magmatic chambers at a scale of a few hundred meters. Waveform inversion from broadband seismic instruments is emerging as a powerful tool for modeling the source geometry of the magma feeding system and its dynamics. An excellent example is the report by Kumagai *et al.* on page 687 of this issue (*2*). The wealth of data provided by these techniques and by other broadband instruments such as strainmeters (see the figure) is beginning to put eruption prediction on a quantitative footing.

The medium- and long-term behavior of high-risk explosive volcanoes remains, however, quite puzzling. Many eruptions of explosive volcanoes have occurred in the past two decades and were consequently relatively well monitored (*3*, *4*). Most of them were preceded by relevant geophysical phenomena, allowing successful forecasting and early warnings. On the other hand, Usu, in Japan, exhibited different eruptive and preeruptive behavior during its four eruptions in the 20th century. The behavior of other volcanoes also does not always follow a clear pattern.

One part of the problem is that systematic geophysical monitoring is performed on only a small percentage (about 10%) of the 1300 active or potentially active volcanoes worldwide. Successful prediction of impending activity has been achieved on basaltic volcanoes such as Kilauea (Hawaii) (*5*) and Sakurajima (Japan) (*6*) and generally for volca-

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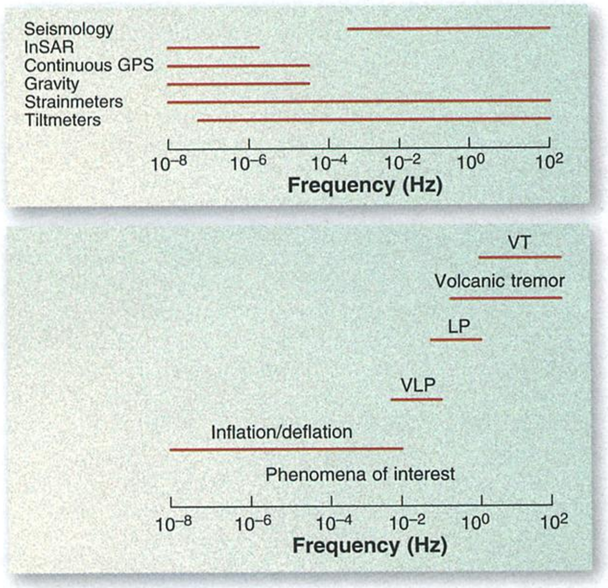

Toward volcanic prediction. Various ground-motion measurement techniques and the corresponding phenomena that can be studied with a variety of instrumentation. VT, volcano-tectonic; VLP, very-long-period; and LP, long period events.

noes characterized by frequent eruptions and a low explosivity index. The data on geophysical precursors are thus still too scarce for a statistically reliable detection methodology on a global basis. Successes are obtained empirically on the basis of eruptive history, physical-chemical properties of magma, and geophysical and geochemical monitoring.

Seismic monitoring is a powerful tool because it allows real-time data analysis. However, the seismic signals on volcanoes are complex and variable. So-called volcano-tectonic (VT) earthquakes are not directly linked to magma movement. Moreover, most data acquisition systems are tuned to the high-frequency band allowing detection of source parameters of the volcano-tectonic events. Most precursors are linked to long-period or very-long-period events, which occur in the frequency band of 1 to 100 s (*7*) and are closely linked to magma fluid dynamics. These movements may occur hours to weeks before the eruptions, constituting more reliable precursors than high-frequency volcano-tectonic earthquakes.

Unfortunately, the sensitivity of seismological instruments is in most cases insufficient for detecting magma and hydrothermal fluids movements. Quantitative methods for analyzing and simulating the behavior of multiphase systems also need further development.

Recent research indicates that broadband seismic radiation is a powerful tool for evaluating not only the source geometry but also the magmatic transport budget (*8–10*). The correct interpretation of these signals allowed the timely evacuation of the 30,000 inhabitants at Rabaul in 1994. This is very important because of the similarities with other calderas, such Campi Flegrei, near Naples, in Italy, or Miyake Island, Japan (*2*).

Another promising technique is the study of phenomena occurring in the frequency band below 10^{-2} Hz, the limit of many traditional seismometers. Data from borehole strainmeters, which can detect strains down to 10^{-10} (three order of magnitudes below GPS) and frequencies down to 10^{-7} Hz, provided important insights into two basaltic eruptions on Hekla, Iceland, in 1991 and 2000 (*11*), and one on Izu-Oshima, Japan, in 1986–87 (*12*), despite the fact that the networks were not designed for volcano monitoring.

The Hekla strainmeters provided the first direct measurements of magma movement, and in 2000, an early warning was officially issued 1 hour before the eruption and was used to alert the nearby airport. On Izu-Oshima, this kind of instrument provided a movie of the vent opening during an eruptive phase in November 1987. Additional instruments of this type have been installed or planned for installation in Mauna Loa, Long Valley, Komagatake, and Vesuvius. This is one of the most promising techniques for monitoring, despite the high costs for planning and borehole installation, which severely restrict their worldwide application.

Several kinds of strainmeters have been developed. In earthquake seismology, these instruments have led to the discovery of slow earthquakes (*13*) and their scaling laws (*14*). Because of their high sensitivity, systematic use of these instruments should allow modeling of the magma and gas transport systems. This will lead to a more quantitative approach in physical volcanology. High-risk volcanoes certainly need more sensitive instruments to model activity, as proposed by Kumagai *et al.* (*2*), and to detect early signals preceding the eruptions.

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PERSPECTIVES: STRUCTURAL BIOLOGY

Actin' Up

Enrique M. De La Cruz and Thomas D. Pollard

The protein actin together with its partner myosin forms the sliding filaments that enable muscle cells to contract. Even though animals with muscles arose relatively recently, actin has been helping eukaryotic organisms to move around for more than a billion years. Protozoa and nonmuscle cells such as macrophages still use actin to move about and to ingest bacteria and other prey. During embryonic development, the actin-based movements of nerve growth cones lay down a spectacular 1 million miles of nerve cell connections in our brains. Myosin proteins motor along actin filament tracks, producing forces that cleave dividing cells into two, transport intracellular vesicles, and power muscle contractions.

It has been known for more than 50 years that actin binds to the energy-releasing molecule adenosine triphosphate (ATP) (*1*). During the polymerization of actin monomers into filaments, ATP is hydrolyzed to adenosine diphosphate (ADP) and inorganic phosphate (P_i). Although ATP and ADP are known to bind to and stabilize actin monomers, it has not been clear how ATP hydrolysis is involved in actin polymerization (*2*). A unique crystal structure of ADP-actin (which, unlike previous actin structures, is not associated with other proteins)—presented on page 708 of this issue by Otterbein and col-

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