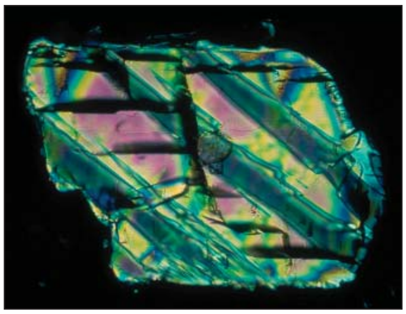
magma. Slightly more than half the magma formed pyroclastic flows (fast-moving avalanches of hot rock fragments and volcanic gases), and the remainder fell in a continent-scale blanket of ash and coarser particles.

Contrary to early models of plinian eruptions—explosive events that form enormous dark columns of tephra and gas high into the stratosphere—pyroclastic flows and fall occurred more or less simultaneously from different parts of the eruption column, fall from the top and flow from the base (*17–19*). The thickest and most voluminous pyroclastic flow deposits were produced by relatively low-energy fountains and spill-over from a widening crater; thinner, more widespread pyroclastic surge deposits were produced by collapse of the high eruption column. Ash began its journey in the tall eruption column and in clouds winnowed from the pyroclastic flows; it fell to Earth from Luzon to India.



Signs of sulfur. This anhydrite crystal in the pumice is indicative of a very sulfur-rich magma.

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Pinatubo nearly exhausted itself on 15 June 1991, vented gently for a few months thereafter, and ended its eruption with a lava dome in July to October 1992. Another batch of basalt had arrived from depth and mixed with dacite, but without the long-term accumulation of volatiles in the dacite, the result was a sluggish last grunt.

As subsurface activity waned, that on the surface remained extremely rapid. Torrential tropical rains washed ~60% of the 1991 deposit off the volcano and set a new world record for annual sediment yield per square kilometer of watershed (*20–22*). Fine ash on steep valley walls was the first to disappear. Rivers then cut deep channels, fed from thousands of tributary rills. Water and erosion triggered explosions, avalanches, and renewed flow of hot pyroclastic debris (*19*). Valleys filled in 1991 with 200 m of fresh deposit were soon deeper than before the eruption (*23*). In a single typhoon, rapid runoff and erosion might deepen and widen the upper reaches of channels by tens of meters and dump tens of millions of cubic meters of hot debris flow on downstream communities. The economic losses and human displacements resulting from these posteruption hydrologic events exceeded those of the 1991 eruption.

While tracking erosion and deposition for hazard assessments, geologists also addressed more fundamental questions. Pinatubo's rivers provide an exceptional natural experiment on river response to sediment loading. High sediment loading led to efficient bedload transport, as in arid regions (*22*). Rocks rolling in flow shallower than their diameters are a geomorphic extreme that points to sediment supply as the main variable in whether stream beds move grain-by-larger-grain or all at once (*24*).

As sediment-laden flash floods (lahars) waned in the late 1990s, the new caldera lake was still changing rapidly. Beginning as a hot puddle in 1991 that could barely survive evaporation and sediment influx, the lake firmly established itself in 1992. By the time a spillway was dug in 2001, the lake was 110 m deep and showing dramatic changes in thermal structure and chemistry that will be fascinating to watch in coming years.

Pinatubo's eruption helped volcanology to grow. It also demonstrated that relatively small investments in pre-eruption monitoring can yield big dividends in scientific insights and life-saving warnings.

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PERSPECTIVES: PINATUBO ERUPTION

The Climatic Aftermath

Alan Robock

The eruption of Mount Pinatubo on Luzon Island, Philippines (15.1°N, 120.4°E), on 15 June 1991 produced the largest stratospheric volcanic aerosol cloud of the 20th century (*1*). In just a few days, about 20 megatons of SO_2 was injected into the stratosphere (*1*). The effect of the eruption on global climate could be felt for years. Surface air temperatures over Northern Hemisphere (NH) continents were cooler than normal by up to 2°C in the summer of 1992 and warmer than normal by up to 3°C in the winters of 1991–92 (see the figure) and 1992–93.

A recent conference (*2*) highlighted the intense research activity in the 10 years since the eruption. From ozone destruction to global changes in atmospheric circulation, the impacts of explosive volcanic eruptions on weather and climate have been elucidated (*3*). Insights into the effects of volcanic eruptions on surface temperatures have helped attribute the warming of the past century to anthropogenic greenhouse gas emissions. Better seasonal forecasts should be possible after the next major eruption.

In the 2 years after the Pinatubo eruption, data from the Total Ozone Mapping Spectrometer (TOMS) and other sources showed unusual O_3 decreases at mid-latitudes and NH high latitudes (*4–7*). Column O_3 was reduced by about 5% in mid-latitudes (*4–6*). The ozone was destroyed by the same mechanism that causes the ozone hole over Antarctica in October each year. Sulfate aerosols produced by Pinatubo and injected into the lower stratosphere provided surfaces for hetero-

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geneous reactions involving anthropogenic chlorine, leading to the chemical destruction of O_3 (*8–10*).

Like the ozone hole, ozone depletion by volcanic aerosols is a recent phenomenon. It is caused by elevated chlorine concentrations in the stratosphere, which only appeared in the last couple of decades because of anthropogenic emissions and will hopefully disappear in a few decades as emissions are increasingly regulated. A lower ozone concentration causes less ultraviolet (UV) absorption in stratosphere. Some UV radiation is backscattered by the aerosols, but the net effect of volcanic aerosols is to increase surface UV (*11*).

During the NH winter of 1991–92, the temperature in the troposphere over North America, Europe, and Siberia was much higher than normal, whereas over Alaska, Greenland, the Middle East, and China, it was lower than normal (see the figure). The unusual cold in the Middle East produced a rare snowstorm in Jerusalem and led to the death of coral at the bottom of the Red Sea (*12*). The same pattern was observed during the winter of 1992–93. Climate reconstructions show that this pattern has followed every large, sulfate-rich tropical explosive eruption of the past century and a half (*13*, *14*).

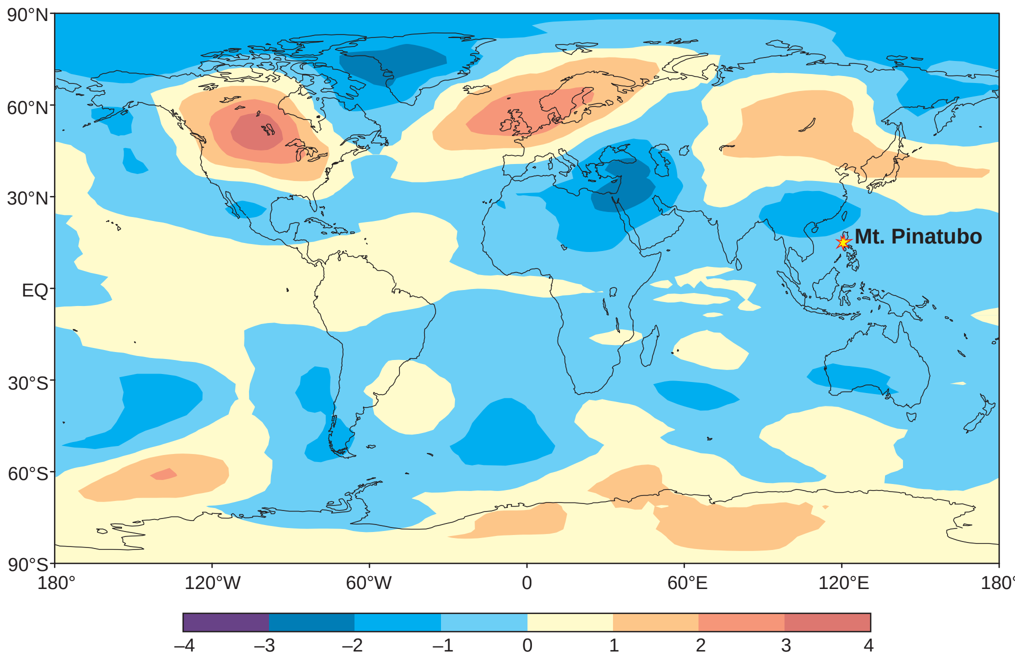
Several volcanic aerosol effects collude to create this pattern of tropospheric temperature changes: warming of the tropical lower stratosphere, ozone depletion at high latitudes, tropical surface cooling, and mid-latitude surface warming (*15*). The pattern is associated with a strong polar vortex and is called the positive mode of the Arctic Oscillation (*16*) [which is closely related to the North Atlantic Oscillation (*17*)]. External stratospheric forcing can push the system into this natural mode of the winter atmospheric circulation relatively easily.

The polar vortex is strengthened by lower stratosphere warming at low latitudes, which is caused by absorption of solar and terrestrial radiation by the volcanic aerosol cloud. Ozone depletion, which in the case of Pinatubo took place mostly at high latitudes in the NH (*15*), also strengthens the polar vortex by causing polar cooling. Climate models have reproduced the observed winter warming when forced with the observed aerosols (*18*) and ozone changes (*15*) after the Pinatubo eruption (*15*, *19*). The results show that the dynamical response of atmospheric circulation to radiative forcing is an important aspect of climate change and highlight the climatic role of the stratosphere (*20*).

Global warming was retarded for several years after the Pinatubo eruption because of the cooling effects of the volcanic aerosols. Simulations of this cooling helped to validate climate models used for global warming. The strong but relatively short-lived climate forcing was used to test and improve climate models and has sharpened our understanding of the climate system. In the past, it has been difficult to attribute global warming to anthropogenic greenhouse gases because observations of climate change show irregular coolings that do not match the expected warming from greenhouse gases. Simulations that include solar forcing and volcanism (*21–23*) accurately simulate climate change before the past century but do not reproduce the 0.6°C warming observed in the past century unless anthropogenic greenhouse gases are considered. These studies have allowed the latest Intergovernmental Panel on Climate Change assessment report (*24*) to give the strongest support yet to the attribution of recent warming to human actions.

The Pinatubo eruption highlighted the limitations of existing satellite sensors and of the latitudinal distribution of vertically pointing lidars. Observations of the tropical stratospheric aerosol cloud and the resulting ozone changes were obscured by the dense cloud. As more lidar stations are installed (there are no good stratospheric lidar stations between 19°N and 23°S) and more sensitive satellite instruments are launched over the next decade, we will be better prepared for the next large eruption.

We can now make much better seasonal and interannual forecasts of the climatic and chemical effects of the next large volcanic eruption, but continuing improvements of the observational system and models will allow us to do even better. For example, we would like to be able to predict the initial distribution and transport of the emission cloud and its chemical and microphysical transformations, rather than wait for observations to tell us where the resulting aerosol cloud goes and how dense it is. Right now, the stratosphere is very clean, and we are poised to observe the clear impacts of the next eruption. Continuing research inspired by the Pinatubo eruption a decade ago continues to improve our capacity to understand and predict its impacts.



After the eruption. Lower tropospheric temperature anomalies for the Northern Hemisphere winter (December 1991 to February 1992) after the 1991 Mount Pinatubo eruption. This pattern is typical after large tropical eruptions, with warming over North America, Europe, and Siberia and cooling over Alaska, Greenland, the Middle East, and China. Data from Microwave Sounding Unit Channel 2R, updated courtesy of J. Christy and now called Channel 2LT (*3*). The nonvolcanic period of 1984–90 was used to calculate the mean.

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PERSPECTIVES: IMMUNOLOGY

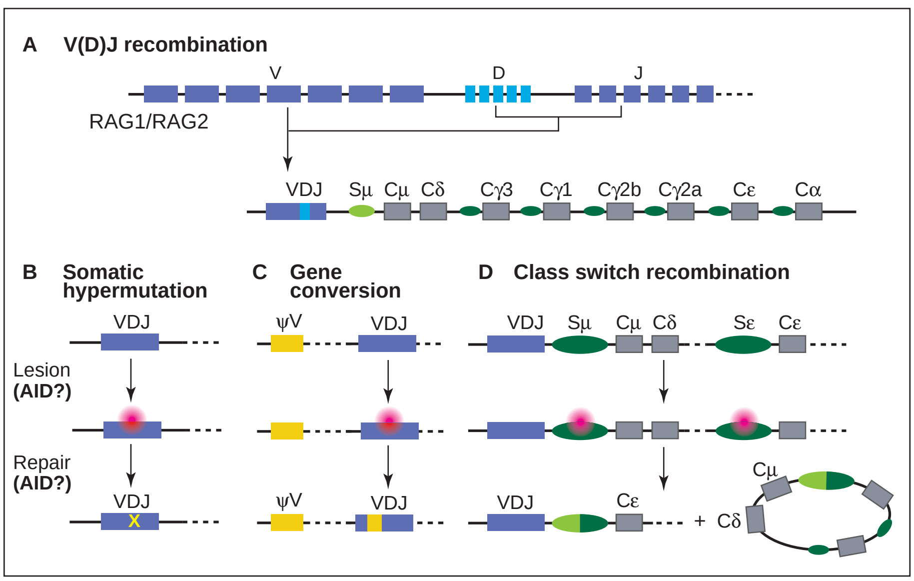
One AID to Unite Them All

Sebastian D. Fugmann and David G. Schatz

Immunoglobulin (Ig) genes, and the antibodies they encode, reign supreme in the realm of genetic diversity. These Ig genes are recombined, rearranged, and mutated by four different molecular processes in B lymphocytes as they develop and mature. Initially, Ig genes are assembled from scattered germline gene elements in a process called V(D)J recombination (see the figure, A). Thereafter, nucleotide changes can be introduced into the assembled variable exon, which encodes the portion of the antibody that makes contact with antigen, through somatic hypermutation (SHM) or gene conversion (GC) (see the figure, B and C). Finally, the constant region of the Ig gene, which determines antibody effector functions, can be swapped in a process known as class switch recombination (CSR) (see the figure, D). The molecular processes underlying SHM, GC, and CSR have proved difficult to delineate. Thus, the recent discovery that one gene, encoding an activation-induced cytidine deaminase (AID), is essential for SHM and CSR in both mice (*1*) and humans (*2*) has generated much excitement. On page 1301 of this issue, Arakawa *et al*. (*3*) neatly complete the picture by demonstrating that GC is also strictly AID-dependent. These authors show that disrupting the *AID* gene in the chicken B cell line DT40 results in a complete block of Ig gene conversion, and that this block can be reversed by reintroducing *AID* into the B cells. This finding is confirmed by Harris and colleagues in their work with DT40 cells, which have the advantages that GC is permanently switched on and that genes can be targeted efficiently (*4*). AID is therefore a pivotal player in the generation of antibody diversity and represents a fascinating point of convergence for the three disparate reactions that drive Ig gene assembly and modification.

Higher vertebrates rely on an extremely diverse repertoire of antibodies to combat infectious pathogens. The initial "preimmune" antibody repertoire is generated during the assembly of Ig genes by V(D)J recombination. In many species, such as sheep, rabbit, and chicken, there is additional preimmune diversification after antibody gene assembly mediated by SHM and/or GC. An encounter between B cells and antigen drives further mutagenesis of Ig variable exons by SHM, and this, coupled with cellular selection events, allows the development of antibodies with very high affinity for the antigen. This "affinity maturation" process is a crucial component of our ability to resist reinfection by the same organism.

The molecular processes underlying V(D)J recombination are well established. First, DNA double-strand breaks are made by the RAG1-RAG2 enzyme complex, and then the broken ends are rejoined in a DNA repair process known as nonhomologous end joining. In contrast, remarkably little is known about SHM, GC, and CSR. It has long been assumed that these reactions, like V(D)J recombination, are initiated by DNA lesions and completed by DNA repair, but only recently has direct evidence for this begun to emerge. SHM has been linked to both DNA double-strand (*5, 6*) and single-strand (*7*) breaks, and does not seem to require nonhomologous end joining for lesion repair (*8*). The DNA double-strand breaks accumulate predominantly in the G_2 phase of the cell cycle (when chromosomes are in the form



Trading places. DNA rearrangements and nucleotide exchanges of the immunoglobulin heavy chain locus during B cell development and maturation. (**A**) In a process called V(D)J recombination, the exon encoding the antigen-binding domain of the antibody is assembled from V, D, and J gene elements (blue boxes). (**B**) During somatic hypermutation (SHM), point mutations (yellow X) are introduced into the VDJ exon through error-prone DNA repair. (**C**) During gene conversion (GC), stretches of nucleotide sequences (yellow boxes) are copied from pseudogene V elements (ψV) into the functional VDJ exon. (**D**) During class switch recombination (CSR), the exons encoding the constant region (C, gray boxes) of the antibody are swapped by recombination events between highly repetitive switch regions (S, green ovals). AID is required for SHM, GC, and CSR, but it is not clear whether this enzyme is involved in the creation or repair of the initial DNA lesion (red circles).

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