Washington state. This generated a rapidly moving suspension flow that travelled 25 km, and is known to have been rather dilute from witness reports and the way trees were blown down. The blast deposit bears some resemblance to low-aspect-ratio ignimbrites[7].

Dade and Huppert[1] have now tested in detail the dilute hypothesis in the case of the Taupo ignimbrite. They use the equations for a dilute, fully turbulent, homogeneous suspension current that they have validated using laboratory aqueous flows. They show that the 80-km runout distance of the Taupo flow, as well as radial variations of deposit thickness and grain size, can be explained by a flow with a solid fraction of 0.3 per cent, volume flux 40 $km^3 s^{-1}$ and travel duration 15 minutes. Neither the huge discharge rate nor the flow speed of 200 $m s^{-1}$ are inconsistent with the known properties of pyroclastic flows. But the ability of a dilute, turbulent flow to transport coarse rock debris such large distances and the poor sorting of the theoretical deposit laid down will go against the intuition of many volcanologists.

So the calculations reproduce the essential features of the Taupo ignimbrite, but some uncertainties remain. There are puzzling discontinuities in radial variations of grain size at Taupo, not explicitly addressed by Dade and Huppert, which are qualitatively consistent with a high-concentration flow model[4]. Dense, high-speed solid–gas flows may be highly heterogeneous[8], however, and cannot yet be modelled, so it is unclear how well they can quantitatively explain the Taupo observations.

Dade and Huppert reinforce their case by showing that clasts of different densities coexisting in the Taupo deposit are in approximate aerodynamic equilibrium with each other, as expected from a low-concentration flow and as observed at Mount St Helens[7]. Ignimbrites characteristically contain both dense rock fragments and frothy, vesicular pumice. During sedimentation from a dilute flow, the largest dense and light clasts deposited at a given site should have the same settling speed in hot gas. In flows of higher concentration, buoyancy forces would permit large pumices to travel further than calculated on aerodynamic grounds alone.

Despite its apparent success at Taupo, I think it would be unwise to extrapolate the dilute flow model to ignimbrites of higher aspect ratio. Many show clear evidence of emplacement as dense, fluidized dispersions. For example, at the Valley of Ten Thousand Smokes in Alaska, the pyroclastic flows of 1912 were so concentrated and sluggish that in one place they were unable to surmount a ridge 25 m high[9]. The common occurrence of ignimbrites that are densely welded over thousands of square kilometres[10] implies efficient heat retention during transport that may be hard to reconcile with dilute flow.

It now appears possible that ignimbrites are generated by a continuum of pyroclastic flows, from small, highly concentrated ones to high-speed types emplaced under dilute, highly turbulent conditions. Quantitative understanding of this spectrum of complex and dangerous two-phase flows presents a major challenge to volcanologists and fluid dynamicists. Dade and Huppert's elegant marriage of mathematics with field observations offers a way forward. □

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GLACIAL CYCLES

Trees retreat and ice advances

Mark Chandler

ONE hundred and fifteen thousand years ago, the Earth began a descent from the warmth of the last interglacial to the frigid climate of the last ice age. What began as a period with air temperatures similar to the present or perhaps slightly warmer, had declined by 21,000 years ago to a state 7–10 °C colder than today. High-latitude temperatures were at least 15 °C colder, and ice sheets more than 1 km thick covered much of North America and large portions of Eurasia above 55° N. The mechanism commonly accepted as initiating the growth of these massive continental ice sheets is the reduction of summertime solar radiation at high latitudes, resulting from cyclical variations in the orbit of the Earth. But many global climate modelling studies have found that the reduction in solar radiation that occurred 115 kyr ago does not, by itself, yield conditions suitable for the maintenance of year-round snow cover. Now, however, climate model experiments reported by Gallimore and Kutzbach on page 503 of this issue[1] show that changing vegetation patterns, specifically the spread of tundra, may have played a prominent role in this reversal of fortunes for the global climate.

In 1989, Rind *et al.*[2] published an article discussing the inability of a particular 'general circulation model' (GCM) to initiate ice-sheet growth using the conditions of 115 kyr ago. Since then it has been shown that most, if not all, GCMs are similarly limited given solar radiation as the sole forcing change[3,4]. Speculation that the record is misinterpreted has been widely dismissed given the considerable independent evidence for rapid ice-sheet growth[5]. Concern that these models lack the appropriate sensitivity to simulate even such large climate changes was more seriously considered, because it has implications for estimating future climate change.

But the unanimity of negative results for ice initiation bolsters the belief that the models are not fundamentally flawed, but rather are missing pieces of the puzzle. The search for these missing pieces has led climate modellers to incorporate other environmental changes into their experiments. Examples include reducing carbon dioxide levels based on ice-core records and using altered sea surface temperatures with the assumption that ocean circulation was somehow affected. Without exception these added forcings have not yielded permanent snow cover over the regions that eventually came to be dominated by ice sheets.

The new GCM experiments[1] show that tundra expansion near the end of the last interglacial may have affected the Earth's albedo enough to help promote glaciation. In their experiments, Gallimore and Kutzbach use a coarse-resolution version of the NCAR Community Climate Model (CCM1) coupled to a simple mixed-layer ocean. The effects of tundra expansion were examined in two steps, to imitate slowly shrinking high-latitude forests. The expansion of tundra is most important to the radiation balance during winter months, because snow lies in a highly-reflecting layer on the open tundra, whereas dense forests are likely to mask it.

Simulations using reductions in solar radiation and atmospheric carbon dioxide content alone failed to produce perennial snow fields except over the permanent ice caps of Greenland and Antarctica. But the expanded tundra dramatically decreases the snow-free period and increases the area over which snow remains throughout the summer, to accumulate during ensuing winters. Over the Keewatin area and Baffin Island, key glacial initiation centres, snow accumulates at a rate of 30 to 50 cm of water equivalent per year. Over thousands of years this would lower sea level by at least as much as isotopic records indicate.

Although the news of a modelling success is encouraging, the authors point out that their model accumulates large amounts of snow in regions that glaciologists believe were relatively ice free during the last ice age. The only other GCM that reported an ability to initiate ice sheets[3] had a similar problem.

Another problem that remains unresolved is how the continental glaciers were able to extend to latitudes south of 60° N. Further north, the extrapolated accumulations would rapidly lead to absurdly thick ice sheets unless the ice began to expand southward across the continents. But in even the most encouraging experiments, the region of perennial snow cover only begins 20 degrees north of the Laurentide glacier's southernmost margin, and the new expanded-tundra experiments have land south of 55° N snow free for over 3 months out of the year. It is difficult to see how the glaciers can have survived so far south. Of course, the ice sheet may create local climatic effects that support continued ice growth. Furthermore, rapid snow accumulation at high latitudes might enable a rapidly flowing glacier to reach the mid-latitudes before melting. But pursuing such hypotheses will require lengthy simulations with a coupled GCM/ice-sheet model.

Whatever the answer, the distinctions between various model results are not nearly as glaring as one might expect from their contrary conclusions. A difference of only one degree in key regions can be the difference between ice-sheet initiation and melting snow. Biases of this magnitude are common in current climate runs and, because the results depend on reaching critical thresholds, disparate conclusions are bound to exist. Given the uncertainties in cloud distributions and sea-ice formation, the sensitivity of the models to comparable forcings is remarkably similar. Unfortunately, as far as ice-sheet growth is concerned, their sensitivity remains inadequate.

Obvious extensions to the latest experiments include using land surface schemes that more realistically, or even interactively, simulate vegetation and ground hydrology interactions. The transformation from forest to tundra is extreme in many respects — not only albedo is altered during such a changeover. Soil moisture, runoff and surface roughness all generate feedbacks that may affect the growth of glaciers. Ocean thermohaline circulation, other greenhouse gases (methane for example), and desert dust aerosols have all been suggested as important influences on ice-sheet initiation and maintenance. Glacial cycles have even been attributed to external mechanisms, such as periodic variation in the flux of interplanetary dust particles.

The effects of most of these factors remain unexamined, and Gallimore and Kutzbach's experiments demonstrate once again that, when it comes to the study of climate change, previously overlooked feedbacks may prove more important than the original instigator of change. □

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NEUROBIOLOGY

Agrin signals at the junction

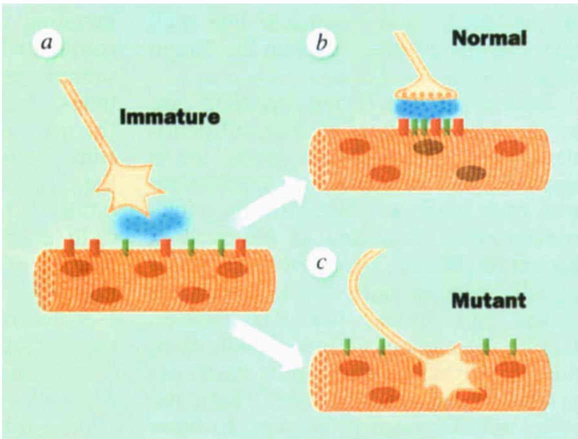
Clarke R. Slater

THE ability of the nervous system to deal with the real world depends on rapid communication between its neurons at synaptic junctions. That communication involves the release of a chemical transmitter from one neuron and its binding to a receptor protein on the next, so the speed of transmission depends on the receptors being concentrated close to the sites of transmitter release.

The control of receptor clustering at synapses during development is believed to involve a second, more leisurely, form of signalling between neurons and their targets. Three papers published in *Cell* on 17 May help to define some of the signals involved. Gautam *et al.*[1] have used gene targeting in mice to show that agrin, a neurally derived protein that induces the aggregation of acetylcholine receptors (AChRs) on muscle cells *in vitro,* is also essential for the formation of neuromuscular junctions *in vivo*. DeChiara *et al.*[2] have used a similar approach to show that MuSK, a muscle-specific protein kinase, is equally essential. Connecting these observations, Glass *et al.*[3] provide evidence that MuSK mediates the response to agrin.

For practical reasons, control of the distribution of synaptic receptors is best understood at the neuromuscular junction, where the principles of chemical synaptic transmission were first elucidated. AChRs are expressed all over the surface of immature muscle fibres but aggregate at the primitive neuromuscular junction soon after the nerve makes contact. The immature AChR cluster requires the presence of the nerve for a few days to acquire stability. After that, the cluster persists if the nerve is destroyed, implying that information adequate to maintain junctional AChR clusters becomes 'built in' to the surface of the muscle fibre during synapse formation.

During the past decade, McMahan and his colleagues have obtained striking support for this view (see ref. 4 for review). They first found that molecules able to cause aggregation of AChRs on cultured muscle cells are bound to the region of the basal lamina, a loosely knit sheath of extracellular material that lies between nerve and muscle. They then identified a family of proteins, some of which account



Proposal for synapse formation at the neuromuscular junction. *a*, In early development, before the motor axon of the nerve has reached the muscle fibre, the fibre lacks local specialization. Muscle-specific protein kinase (MuSK, red), acetylcholine receptors (AChR, green) and other proteins are uniformly distributed along the fibre. The motor axon releases agrin (blue), which activates MuSK at the site of contact. *b*, In later development, agrin accumulates in the basal lamina of the synapse. MuSK, AChRs and many other molecules (not shown) become concentrated in the mature synapse, due in part to local transcription from synaptic nuclei (shaded). The motor axon differentiates a presynaptic terminal in response to unidentified signals from the muscle fibre. *c*, In mutants lacking agrin or MuSK, the motor axon fails to induce postsynaptic specialization in the muscle fibre; the fibre does not produce the stop/differentiate signal, so motor axons wander over the muscle surface without differentiating.