

coordinated fashion through ATR-dependent phosphorylation.

Almost all DNA-repair pathways process DNA damage through extensive RPA-ssDNA intermediates. Pathways such as base excision repair (BER) that do not generate significant RPA-ssDNA intermediates appear invisible to the checkpoint system (7). Stalled replication forks are known to expose extended regions of RPA-ssDNA (8). Thus, the ATR-dependent checkpoint can respond to multiple DNA damage and replication problems by recognizing RPA-ssDNA, a common topological intermediate. Importantly, this biochemical understanding of damage detection will help lay to rest a myriad of misunderstood observations linking specific DNA-processing enzymes (such as helicases, nucleases, repair and replication proteins) to checkpoint signaling. Any mutation influencing DNA metabolism can potentially influence the extent of RPA-ssDNA generation. This will have a corresponding, but indirect, impact on the ATR-dependent checkpoint pathway.

Is RPA-ssDNA the sole activator of the ATR-dependent checkpoint? Certainly, reports that Ddc2 (ATRIP) directly binds to DSBs (9) are not supported by Zou and Elledge's analysis. DSBs are the most dangerous initial lesion to a cell, and it is intriguing that the parallel ATM-dependent checkpoint pathway responds specifically to DSBs. ATM-dependent signaling requires the recombination repair protein complex Mre11-Rad50-Xrs2 (MRX), and both ATM and MRX associate with DSB-damaged chromatin. Does the ATM pathway respond directly to DSBs (before the generation of RPA-ssDNA) by directly binding to DSB-MRX complexes, or is there also a requirement for RPA-ssDNA for ATM activation? Possibly, MRX fulfills an ATRIP-like function for ATM, allowing it to respond specifically to RPA-ssDNA generated by the MRX-dependent nucleases. Recent data suggesting that ATM is activated by chromatin distortions, independently of DNA breaks (10), do not exclude a role for RPA-ssDNA because chromatin distortion may expose ssDNA.

Zou and Elledge demonstrate that a simple paradigm for DNA-damage signaling is conserved from bacteria to humans. Prokaryotes sense RecA-ssDNA, whereas eukaryotes sense RPA-ssDNA. Detecting multiple DNA perturbations, particularly those caused by replication stress, is vital to coordinate DNA repair with cell cycle progression and apoptosis. Such coordination is essential for survival of cells and the whole organism. That ssDNA underlies damage detection shows that, in the end, the beginning of signaling has a simple explanation.

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GEOCHEMISTRY

How Old Is Planet Earth?

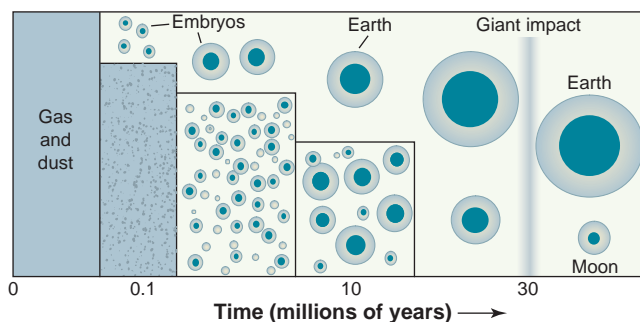
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Recent reports (1–4) on the tungsten (W) isotope composition of meteorites have led to a completely revised time scale for the formation of the terrestrial planets. The results show that most of planet Earth had formed within ~10 million years (1, 2) after the formation of the solar system some 4567 million years ago (when the first solid grains formed in the solar nebula) (5). The Moon-forming event happened ~30 million years after solar system formation, when Earth was fully grown (2, 3).

The decay of the hafnium isotope ^{182}Hf (with a half-life of 9 million years) into ^{182}W is the best “clock” we have for tracing the formation of terrestrial planets during the first 50 million years of solar system history. The behavior of these elements during metal-silicate separation, which occurs during the formation of planetary cores, is well understood.

Hafnium is a lithophile element (it has a strong affinity for silicate liquid) and stays entirely in the silicate mantle (and crust) of the planet. Hence, the mantle is where ra-

dioactive decay of ^{182}Hf to ^{182}W occurs. In contrast, tungsten is siderophilic (it has a strong affinity for iron melt), and about 90 to 95% of it is partitioned into the metal when metal and silicate separate in the core-forming process. After 50 million years, the Hf-W chronometer is a dead clock because almost all ^{182}Hf has decayed, but for the first 50 million years of solar system history, it is ideal for tracking a planet's growth.



The formation of Earth. The first new solid grains formed from the gas and dust cloud called the Solar Nebula some 4567 million years ago. Within 100,000 years, the first embryos of the terrestrial planets had formed. Some grew more rapidly than others, and within 10 million years, ~64% of Earth had formed; by that time, proto-Earth must have been the dominant planet at 1 astronomical unit (the distance between Earth and the Sun). Accretion was effectively complete at 30 million years, when a Mars-sized impactor led to the formation of the Moon. The figure is not to scale.

In the earliest work on this chronometer (6, 7), we found that the solar system's initial $^{182}\text{W}/^{183}\text{W}$ value was about 3 to 4 parts in 10,000 lower than the present terrestrial value, and inferred a relatively short time scale for the formation of Earth. This short time scale was challenged by Lee and Halliday (8), who reported that Earth and chondritic meteorites have essentially identical $^{182}\text{W}/^{183}\text{W}$ values to within 20 parts per million—indicating that Earth formed relatively late, after the decay of ^{182}Hf (when the Hf-W clock was dead). They reported an age of core formation within Earth corresponding to 60 ± 10 million years after solar system formation. This age has been widely cited.

However, because the clock was dead by this time, it should have been reported as any time between 50 million years after solar system formation and the present.

Last year, three groups reported that $^{182}\text{W}/^{183}\text{W}$ in chondrites is lower than that of Earth by 2 parts in 10,000, and thus intermediate between the initial solar value and that of Earth today (1–4). These new results have fundamentally changed the way in which the

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Hf-W chronometer can be used, because they demonstrate that ^{182}Hf was live when Earth formed.

However, the groups drew different conclusions from their data. Shoenberg *et al.* (3) and Kleine *et al.* (4, 9) concluded that Earth's core formed at 30 million years, whereas we pointed out that the total time scale for Earth's formation is 30 million years and that most of the planet must have formed within 10 million years (1, 2). Shoenberg *et al.* (3) considered core formation to be a catastrophic event rather than a continuous process during accretion. Kleine *et al.* (4) suggested that the time scale of core formation decreases with decreasing planet size.

This brings us to the question of how to define Earth's age in this context (see the figure). In some way it can be said to be the same as the age of the solar system—defined as the time of formation of the oldest known accreted objects at 4567 million years (5)—because models of planetary accretion imply rapid initial material coagulation that leads to protoplanetary “embryos” on a time scale of only 100,000 years (see the figure). A Mars-sized object that later became Earth may already have existed at this early time.

Another way of defining Earth's age is to use the “mean age,” when the planet had accumulated ~64% of its mass. The con-

cept of a mean age implicitly assumes, in agreement with most accretion models, that the growing Earth can be identified from very early times with an embryo that grows much faster than other nearby objects, which are eventually accreted to the planet. Accretion models suggest that the rate of accretion is approximately exponential. In this case, the mean age can easily be determined from the W isotope composition in a system that is fractionated by core formation/accretion (6). Based on this approach, Earth's mean age corresponds to ~10 million years after solar system formation (1, 2) (see the figure).

Finally, Earth's age could refer to the “end” of Earth's accretion, when Earth had grown to about its present mass. However, because the accretion process had a long tail and is technically still continuing today, this is not a well-defined point in time. The best choice for the end of accretion is probably the final major event in Earth's accretion: the formation of the Moon by a Mars-sized impactor. This time is constrained by the new W isotope data to be ~30 million years after the formation of the solar system (1–4).

Furthermore, the new W isotope data (1–4) have established the initial $^{182}\text{Hf}/^{180}\text{Hf}$ of the solar system as $\sim 10^{-4}$. Wasserburg *et al.* have shown (10) that such a high initial abundance will only occur if several different types of supernovas contributed to the

materials from which the solar system was made. One of these sources (SNACS, supernova actinide source) must have overproduced heavy isotopes such as actinides and ^{182}Hf relative to lighter isotopes such as ^{129}I .

Precise measurements of W isotopes are among the most difficult measurements ever attempted by geo- and cosmochemists. As shown above, these studies are extremely worthwhile, even if some results turn out to be incorrect. It is important that several groups continue to perform such measurements and challenge each other's results. A few precise and well-substantiated measurements are more informative than a large body of data with lower precision and accuracy.

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PLANT SCIENCE

Surprises Inside a Green Grass Genome

Michael Bevan

Among the dozens of genome sequences published each year, those of only two organisms have achieved iconic status—those of humans and of rice (*Oryza sativa*). The discoveries to be made from the human genome can be translated into improved health worldwide, and those from rice can be implemented to provide a sustainable supply of nutritious food for the world's growing population.

Draft genome sequences of two subspecies of rice (*indica* and *japonica*) were published last year (1, 2) and now the high-quality, fully annotated sequence of *japonica* rice is on target for completion in 2004. The report on page 1566 of this issue (3) de-

scribes the complete sequence of rice chromosome 10, which, at 23 Mb, is the shortest of the 12 chromosomes of the 430-Mb rice genome. The sequences of chromosome 1 (4) and chromosome 4 (5) have recently been completed, providing more than 100 Mb of high-quality annotated sequence. The description of the chromosome 10 sequence extends our knowledge of the rice genome, as extensive comparisons and generalizations can now be made. What are the general features of the rice genome emerging from this work? Surprisingly, analysis of chromosome 10 reveals a quite different picture of the rice genome than that gleaned from whole-genome shotgun sequencing of the *indica* (1) and *japonica* (2) rice genomes. Although the total gene count of about 60,000 predicted from the completed sequence is in close agreement with the 59,885 predicted from the *japonica* whole-

genome shotgun sequence (4), in fact the actual gene composition revealed by the high-quality sequence is going to be quite different. About twice as many genes can be predicted from the high-quality sequence as from the complete genome shotgun sequence because the coverage is more complete and because more than half of the genes predicted from whole-genome shotgun sequencing of *indica* were interrupted, leading to multiple predictions. These features suggest that complete genome sequences will quickly become the gold standard for both public and corporate research, and they eloquently justify the great effort, precision, and time required to obtain contiguous and anchored sequence.

What about post-genomics research in rice? Two major research areas are foreseen. The first will exploit the abundant resource of new rice- and grass-specific proteins revealed by complete sequencing. Only half of the predicted proteins in rice are similar to the predicted proteins of the model plant *Arabidopsis* (a member of the *Brassica* family). Thus, rice functional genomics should yield a wealth of information about grass-specific proteins. Insertional mutagenesis is being developed for rice—based on, for example, the endogenous retroelement

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