

providing the first-ever conjunction of two spacecraft at an outer planet. Nearly simultaneous measurements were also made by the Hubble Space Telescope and the Chandra X-ray Observatory from Earth orbit. Because Galileo's high-gain antenna failed to open, the spacecraft has very limited communication to Earth and cannot provide the larger picture of Jupiter meteorology. Cassini scientists and engineers took this opportunity to take simultaneous measurements with the Galileo spacecraft, to provide a long continuous look at the Jupiter system, and to test their experiments in



An active atmosphere. Jupiter's atmosphere has a banded appearance with many atmospheric phenomena, including the Great Red Spot seen on the lower right. Cassini's flyby in late 2000 provided global movies of the planet's meteorology.

preparation for the 4-year tour of the Saturn system. The first Cassini imaging results are presented by Porco *et al.* in this issue (1). Cassini measurements of the Jupiter radiation environment, which complement the imaging results reported here, have been published previously (2).

During the Jupiter flyby, the Cassini camera system collected 26,000 images between 1 October 2000 and 22 March 2001. The main purpose of the flyby was to accelerate the spacecraft on to Saturn. At the closest approach of 9.72 million km (136 times Jupiter's radius), the images have a resolution of 58 km, not as good as the best images sent back by Voyager (during its

1979 flyby) and Galileo. But Cassini spectacularly succeeded in providing 6 months of global, continuous viewing of Jupiter's atmosphere.

It is too soon to say whether these data can answer the question of the ultimate source of the bands and eddies on Jupiter (see the second figure). Do these arise from small convective storms gradually aggregating into the large, organized motion? Do the larger storms thus "feed" on this energy source to sustain their long existence? The "Great Red Spot" is a centuries-old hurricane that could hold several Earths. The Cassini images show it gobbling up several smaller storms (1), supporting this scenario.

Cassini's observations of Jupiter's polar region have been assembled into a movie that shows surprising new phenomena. Toward the poles, Jupiter's banded appearance fades, and hundreds of interacting vortices are seen. Small-scale features north of 60° latitude

grow and disappear in a period of weeks. A large dark oval—as big as the Great Red Spot—grew, developed a bright core, began to circulate clockwise, and finally elongated and thinned, gradually disappearing. This storm may have been triggered by an event in Jupiter's magnetosphere: Its location coincides with the region where particles from Jupiter's radiation belts enter the atmosphere (3), causing bright aurorae (like the northern lights on Earth). Cassini is now planning comparable observations of Saturn's polar regions to seek similar phenomena there.

The Cassini cameras observed aurorae on the back side of Jupiter while simultane-

ous measurements were made by Hubble from Earth orbit. These data confirm that the auroral region is larger on the night side, as expected from variation in the pressure of the solar wind. The moons Io and Europa were photographed when eclipsed from the Sun by Jupiter, showing visible glows from electrons that strike their thin atmospheres. These observations will be fruitfully compared with those from Hubble to better characterize this atmospheric phenomenon (4).

Movies of Jupiter's very faint and thin rings confirm that small moons like Metis and Adrastea are the immediate source of the ring particles. The meteoritic bombardment of these objects knocks off dust particles that then form the visible ring around Jupiter. Porco *et al.* make good use of the particular angles at which Cassini observed to argue that the ring particles are not spherical, as was previously assumed.

The Cassini Jupiter flyby was a great success, helping to prepare for the Cassini Saturn mission and providing key data sets (including images and movies) about the meteorology of Jupiter, its moons, magnetosphere, and ring system. Saturn has only been visited briefly by Pioneer (1979) and the two Voyager spacecrafts (1980, 1981). The planned 4-year orbital mission will allow long-term studies and follow-up observations of new discoveries. The Jupiter results provide some hints of the spectacular new findings that await Cassini when it reaches Saturn.

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BOTANY

State Transitions—A Question of Balance

John F. Allen

Green plants and algae use a process of photochemical energy transduction called photosynthesis to harness light energy to make the energy-rich molecule ATP. Within their chloroplasts, light energy captured by chlorophyll photopigments is transformed into an electrochemical potential, which raises the energy of an electron; the subsequent "fall" of the electron

back to its original state releases energy that is used to make ATP. Plants must tune photosynthesis to changing light conditions, and they do this with kinases that phosphorylate (add phosphate groups) to proteins of the photosynthetic machinery. The light-harvesting complex II (LHCII) is found in the chloroplasts of all plants and green algae, and accounts for about half of the chlorophyll molecules in nature. It tunes energy conversion to the wavelength of light in a balancing act known as state transitions. For over 20 years, the redox-controlled kinase that phosphorylates proteins in the

LHCII and thus drives state transitions has been eagerly sought. Despite ingenious biochemical experiments, the results have invariably been ambiguous, yielding interesting new proteins but leaving the identity of the LHCII kinase shrouded in mystery (1). Enter Depège *et al.* (2) on page 1572 of this issue, with their report of a new LHCII kinase. Using a genetic approach to screen for mutants of the green alga *Chlamydomonas reinhardtii*, they identify a new serine-threonine protein kinase in the chloroplast thylakoid membranes. They call their kinase Stt7 (for state transition, thylakoid) and demonstrate that it is required for the phosphorylation of the LHCII protein complex.

Both light and dark reactions comprise the energy conversion steps of photosynthesis. During the former, light energy drives the movement of an electron from a reluctant donor to a reluctant acceptor. This is followed by dark reactions during which the electron is returned to its lowest energy state

The author is in the Department of Plant Biochemistry, Center for Chemistry and Chemical Engineering, Box 124, Lund University, SE-221 00 Lund, Sweden. E-mail: john.allen@plantbio.lu.se

in order to make ATP and, eventually, to fix carbon dioxide. In the 1930s, experiments with short flashes of light of different intensities revealed that there is a surprising excess of chlorophyll molecules involved in the primary events of photosynthesis (3). In a “photosynthetic unit” of about 300 chlorophylls that work together to absorb each quantum of light energy, only one chlorophyll molecule converts energy into a stable chemical form in a protein complex called the “reaction center.” The remaining chlorophylls are “light-harvesting” pigments that keep the reaction center supplied with light energy quanta at a rate enabling one quantum to be converted about every 60 ms at normal light intensities. Subsequent experiments revealed that the wavelength dependency of photosynthetic yield is caused by two different but connected photosynthetic units—photosystem I and II (3). Photosystem II supplies electrons to photosystem I, and their serial connection means that the rate of electron transport between the two photosystems must be equal. Thus, for maximal photosynthetic efficiency, the rates of delivery of quanta to the two reaction centers must also be identical.

In 1969, using two experimental algae—*Chlorella pyrenoidosa* and *Porphyridium cruentum*—with different light-harvesting pigments, two laboratories reported independently that absorbed light energy is redistributed constantly between photosystems I and II by means of state transitions (4). Under light conditions that favor photosystem I (light 1), the fluorescence emission from chlorophyll increases over the course of a few minutes, indicating that the surplus energy of photosystem I has been redirected to the rate-limiting fluorescent photosystem II. In the resulting “light-1 state” (state 1), absorbed light energy is distributed equally between photosystems I and II. But under light conditions that favor photosystem II (light 2), there is a sharp rise in chlorophyll fluorescence as photosystem II becomes saturated with quanta. During the next few minutes, fluorescence falls as excess light 2 is used up by the now rate-limiting photosystem I. In the resulting “light-2 state” (state 2), an equal balance also is achieved, this time because a fraction of the light-harvesting chlorophylls of photosystem II are moonlighting—they have been redeployed to collect quanta for photosystem I.

What causes the transition between states 1 and 2? Plastoquinone is one of the electron carriers that connects photosystem I with photosystem II (see the figure). Under light 2 conditions, electrons enter the plastoquinone pool faster than they leave it and plastoquinone becomes reduced. Reduction of plastoquinone activates a thylakoid protein kinase that Depège *et al.* postulate may be Stt7. This enzyme catalyzes phosphorylation of LHCII proteins, which then leave photosystem II and join photosystem I (5). The imbalance in energy distribution is therefore corrected and plastoquinone is restored, in state 2, to a condition of redox poise. Conversely, light 1 causes photosystem I to extract electrons from plastoquinone faster than they arrive from photosystem II. When plastoquinone is thus oxidized, the kinase is switched off, LHCII becomes dephosphorylated by an LHCII

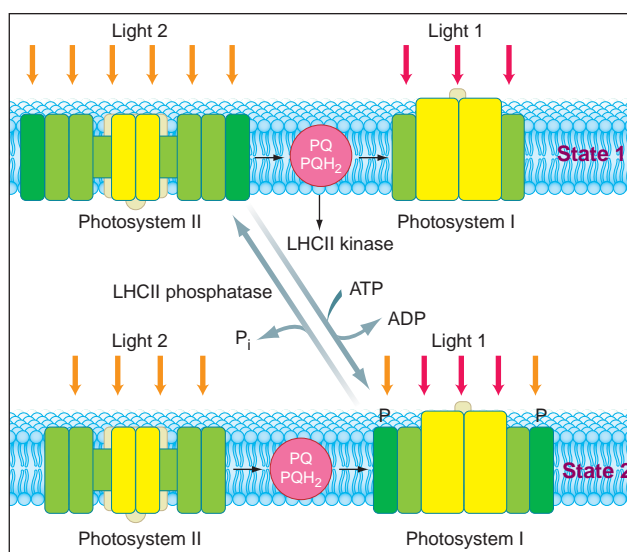
phosphatase, and balance is restored in state 1 as LHCII returns to photosystem II.

To screen a *Chlamydomonas* DNA library for state transition mutants, Depège *et al.* (2) measured the fluorescence emission of chlorophyll in the cell colonies. Rochaix’s laboratory described such mutants a few years ago. Now, Depège and colleagues conclusively identify the *stt7-1* and *stt7-2* mutants as incapable of undergoing the state 2 transition with concomitant decreased phosphorylation of LHCII (2). Both mutants carry mutations in the nuclear gene encoding the Stt7 protein of chloroplast thylakoid membranes. From its sequence, this protein is predicted to be a serine-threonine kinase. The 754 amino acids of Stt7 include an amino-terminal 41-amino acid chloroplast transit peptide and a putative single membrane helix that is located between the transit sequence and the catalytic domain. There

are two cysteines similar to the site of action of the redox regulatory protein thioredoxin. Stt7 has clear orthologs in the model plant *Arabidopsis thaliana* and a paralog Stt1 (state transition–like) in a *Chlamydomonas* expressed sequence tag collection (2). Further work is needed to confirm that Stt7 is required for state transitions in other species, and to characterize Stt1. Future investigations should be aided by the availability of *Arabidopsis* plants engineered to be deficient in Stt7 (2).

It may be that Stt7 forms just one link in the redox signaling pathway that underpins the state transitions of photosynthesis, perhaps working together with other thylakoid-associated kinases (5). The core event—occupancy of a binding site by reduced plastoquinone—probably occurs in the cytochrome *b₆f* complex which, like plastoquinone, connects photosystem I with photosystem II (6). These initial steps in signal transduction may be common to both LHCII-containing cells and to cyanobacteria and red algae, which have a different kind of light-harvesting antenna. It is possible that Stt7 is specific to LHCII-containing organisms.

There is also a long-term balancing act in play because plastoquinone controls the relative rates of transcription of photosystem I and II reaction center genes (7). This mechanism serves to balance the absolute stoichiometry of photosystem I relative to photosystem II, not just their delivery of light quanta to



Transitions between states. During photosynthesis, the LHCII kinase phosphorylates the LHCII protein complex and is required for the transition from state 1 to state 2. The LHCII phosphatase dephosphorylates LHCII and is required for the transition from state 2 to state 1. The two photosynthetic units, photosystems I and II, have central reaction center domains (yellow) that drive electron transport (blue) into and out of the pool of plastoquinone (PQH₂, reduced plastoquinone; PQ, oxidized plastoquinone). The reaction centers harness light energy, and each works optimally with different wavelengths of light (light 2; light 1). Each photosystem has its own light-harvesting protein pigment complexes (light green) to collect and distribute light energy to the reaction centers. There is also a mobile light-harvesting complex, LHCII (dark green), that serves to collect light for photosystem I in its phosphorylated form (P, phosphate group), and for photosystem II in its dephosphorylated form. The molecular basis of the transition from state 1 to state 2 is redox activation of the LHCII kinase, which could be Stt7 itself or a target of Stt7. This activation takes place when plastoquinone becomes reduced because photosystem II moves electrons slightly faster than photosystem I. Conversely, the molecular basis of the transition from state 2 to state 1 is redox inactivation of the LHCII kinase; this occurs when plastoquinone becomes oxidized because photosystem I moves electrons faster than photosystem II. In the state 1 transition, the LHCII phosphatase reaction restores the ability of LHCII to deliver light energy to photosystem II.

PERSPECTIVES

preexisting reaction centers. This redox control of transcription may be the prime reason why the chloroplast genome retained the genes of its cyanobacterial ancestors.

Future prospects include better understanding of how LHClI phosphorylation affects the dynamic architecture of photosynthetic membranes: both local structural changes at atomic resolution (4) and supramolecular rearrangements of reaction center, light-harvesting, and electron-transfer elements (8–10). With mutants of signal transduction components such as Stt7 re-

searchers can now dissect out the structural consequences for target proteins from an intriguing but mechanistically poorly resolved set of integrated responses. State transitions in photosynthesis may be a specialist evolutionary application of chloroplast redox signaling (7), guided molecular recognition (9–10), and membrane protein trafficking (6). With the characterization of the *Chlamydomonas* Stt7 mutant by Depège and colleagues, researchers now have another tool with which to take state transitions apart and see the stuff of which they are made.

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ASTROPHYSICS

Precision Cosmology? Not Just Yet . . .

Sarah L. Bridle, Ofer Lahav, Jeremiah P. Ostriker, Paul J. Steinhardt

The recent announcement by the WMAP satellite team of their landmark measurements of the cosmic microwave background (CMB) anisotropy (1–3) has convincingly confirmed important aspects of the current standard cosmological model. The results show with high precision that space is flat (rather than curved) and that most of the energy in the universe today is “dark energy,” which is gravitationally self-repulsive and accelerates the expansion of the universe. The evidence is independent of supernovae results (4, 5).

The measurements strongly indicate that the amplitudes of spatial variations in density and temperature that seeded the formation of galaxies were roughly independent of length scale, adiabatic (all forms of energy have the same spatial variation), and followed a Gaussian distribution—just as predicted by the standard Big Bang inflationary model. WMAP heralds a new age of precision cosmology with careful error analysis, tightly constraining many key parameters (6). For example, the lifetime of the universe has been determined to be $13,400 \pm 300$ million years (6). Furthermore, WMAP’s new measurement of the CMB polarization as a function of angular scale shows that the epoch of cosmic reionization—associated with the formation of the first stars—had already occurred when the universe was several hundred million years old.

At the same time we celebrate this triumph, it is important to recognize that im-

portant issues remain. For example, it is not yet clear whether the spectrum of temperature fluctuations is truly consistent with inflation. The spectrum is roughly scale-invariant, but there are hints of peculiarities, and a key inflationary prediction—the presence of gravitational wave effects—has not yet been observed.

We also do not know whether dark energy is due to an unchanging, uniform, and inert “vacuum energy” (also known as a cosmological constant) or a dynamic cosmic field that changes with time and varies across space (known as quintessence). “Dark matter,” which is gravitationally self-attractive, also remains mysterious: We do not yet know its nature, nor are we certain about its density or the amplitude of the initial ripples in its distribution.

Today’s standard theoretical paradigm is the inflationary Big Bang model. According to this picture, the universe began in a state of nearly infinite temperature and density and almost immediately entered a phase of rapid, accelerated expansion (“inflation”). This expansion smoothed out the distribution of energy, flat-

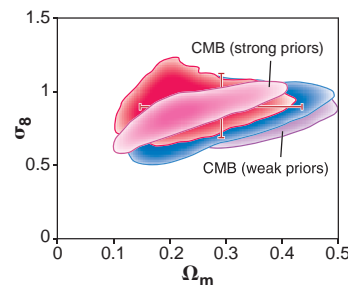
tened any initial warp or curvature in space, and created tiny variations in density. To transform these density variations into the gravitationally collapsed, complex structures we see today, it is essential that there be “dark matter” as well as ordinary (baryonic) matter. Finally, we need dark energy to account for the measured total energy density and to explain the current cosmic acceleration.

Some of the WMAP results—the flatness of space, the near scale-invariance, adiabaticity, and Gaussian distribution of the density perturbations (7), the density of baryons, the age of the universe, and perhaps the early formation of the first stars—are based on WMAP alone and are consistent with the standard model. Because the CMB is a direct

image of the early universe and its interpretation entails simple, well-understood physical principles, these results are robust.

On the other hand, some important issues can only be addressed by combining WMAP data with other cosmological measurements. These conclusions should be viewed more cautiously because the result depends sensitively on the choice of additional data.

For example, by combining data, a significant deviation from a perfectly scale-invariant ($n = 1$) spectrum was found (8). According to the best-fit WMAP combined analysis (8), n runs from 1.1 on the largest scales to < 0.9 on the smallest scales probed, a deviation that disagrees with the simplest and most natural inflationary models (9). These results cast a pall over the inflationary para-



CMB constraints on Ω_m and Ω_{de} . The pink contour corresponds to a “strong prior,” which marginalizes over uncertainties in the Hubble constant, baryon density, and spectral index of primordial fluctuations, but assumes that other parameters are perfectly known, including the optical depth to reionization, $\tau = 0.17$. The other contours are revised limits that include the uncertainty in the equation of state of dark energy (blue; $-1 < w < -0.7$) or τ [red; in agreement with the WMAP alone constraint from (6), shown by the red cross]. The “weak prior” (purple) allows both of these degrees of freedom. All contours are 95% confidence limits; shading corresponds to probability. We used WMAP temperature and polarization data (2, 3, 12) and small-scale measurements from (13–15) and performed the calculations with CosmoMC (16).

S. L. Bridle, O. Lahav, and J. P. Ostriker are at the Institute of Astronomy, Madingley Road, Cambridge CB3 0HA, UK. E-mail: sarah@ast.cam.ac.uk P. J. Steinhardt is in the Department of Physics, Princeton University, Princeton, NJ 08544, USA.