Translocation in Action

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this effect depends on how the two species differ in their ability to colonize bare soils, stabilize soils, and affect nutrient, water, and carbon cycles. In fact, given their genetic differences, the two species would be better placed in different families rather than in the same genus. However, the little research done has focused on *M. vaginatus*, with no work beyond description on *M. steenstrupii*, because its importance in biocrusts has not been recognized (*8*). *M. steenstrupii* constitutes a much more diverse phylogenetic clade than *M. vaginatus* (*9*), and it is likely to be much more genetically and functionally diverse. Renewed efforts should be made to characterize it in all its complexity.

There is also little information to date on the ecological consequences of changing the composition of the nitrogen-fixing cyanobacteria in biocrusts. Garcia-Pichel *et al*. did not directly address biogeographic patterns in these species, but their data show that *Scytonema* sp. appears favored at sites with higher temperatures and *Tolypothrix* sp. at sites with lower temperatures. Possible outcomes of replacing *Tolypothrix* sp. with *Scytonema* sp. include alteration of nitrogen, phosphorus, and carbon cycles. Again, most research has focused on one species, the ubiquitous *Nostoc*, with little information available for either *Scytonema* or *Tolypothrix*.

This lack of research also hampers efforts to actively restore disturbed biocrusts. Most attempts to cultivate and inoculate soils with cyanobacteria to "kickstart" soil stabilization and restoration in areas degraded by human impact use *M. vaginatus* and sometimes *Nostoc*. These efforts are surely at risk of failure if the site should be inoculated with *M. steenstrupii* and *Scytonema* (or possibly other species) instead, because cultivation, inoculation, and/or postinoculation techniques could differ substantially among various species. These situations thus call for a better understanding of which species are currently present at a site and their physiological tolerances.

Chemolithotrophic bacteria and Archaea involved in the nitrogen cycle (*10*) and biocrust fungi (*11*) are some other examples of potentially important groups that we know little about but that may also play pivotal roles in the structure and function of biocrusts and many other ecosystems. It is time to tackle the difficult job of identifying the relevant microbes and their distributions and of establishing their functional roles to enable better management and restoration of dryland ecosystems.

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Supplementary Materials

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Movie S1

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BIOCHEMISTRY

Translocation in Action

Structures of translocation intermediates reveal how tRNA molecules move through the ribosome during protein synthesis.

Marina V. Rodnina

Ribosomes are macromolecular factories that translate the information encoded in messenger RNA (mRNA) into the amino acid sequence of proteins. Each time an amino acid has been transferred to the growing peptide chain, the mRNA and two transfer RNAs (tRNAs) move through the ribosome one codon at a time. This movement—called translocation—is promoted by elongation factor G (EF-G). Three papers in this issue, by Tourigny *et al*. on page 1542 (*1*), Pulk and Cate on page 1544 (*2*), and Zhou *et al*. on page 1543 (*3*), present high-resolution structures of translocation intermediates and provide insights into the underlying mechanism.

The translocation process occurs within milliseconds and entails a large number of structural rearrangements. During translocation, the small and large ribosomal subunits (SSU and LSU) rotate relative to each other (*4*). The SSU undergoes internal motions (collectively called swiveling) of its head domain relative to the body (*5*). The tRNAs move from the A (aminoacyl) to the P (peptidyl), and from the P to E (exit) binding sites, and there are several intermediate positions that the tRNAs can adopt spontaneously (*4*, *6*, *7*) (see the figure). All these rearrangements are rapid and only loosely coupled, making it extremely challenging to obtain structural data on the trajectories of the movements.

To trap EF-G on the ribosome, all three groups (*1*–*3*) used nonhydrolyzable analogs of guanosine 5′-triphosphate (GTP) and placed a single tRNA on the mRNA codon in the P site of the ribosome. The structures show that the ribosome is trapped in a chimeric intermediate state (see the figure, panel B) that differs from the ground states before (panel A) and after (panel C) translocation. This means that the tRNAs move through a series of intermediates not only on the LSU (*7*) but on the SSU as well (*8*), providing new insight into the mechanics of tRNA translocation. One interesting possibility is that GTP hydrolysis by EF-G is required to promote the backward rotation of the SSU head domain and the movement of the tRNA and mRNA into the posttranslocation state (see the figure, panel C). The results of experiments with a guanosine triphosphatase (GTPase)–deficient EF-G mutant appear to be consistent with this idea (*9*).

EF-G is a large, five-domain GTPase that changes its conformation in response to GTP hydrolysis (see the figure). Without GTP hydrolysis, translocation is slow and the release of EF-G from the ribosome is blocked (*10*). Like all GTPases, EF-G has the mobile switch 1 and 2 elements in its GTP-binding domain I. The switch regions are disordered in the unbound EF-G and become ordered in the complex with the ribosome. This transition causes reorientation of the EF-G domains, such that the tip of domain IV moves and the intermediate state of the ribosome is stabilized (see the figure, panel B).

The ribosome on its own allows the tRNAs to move in the forward or backward direction. EF-G provides the directionality

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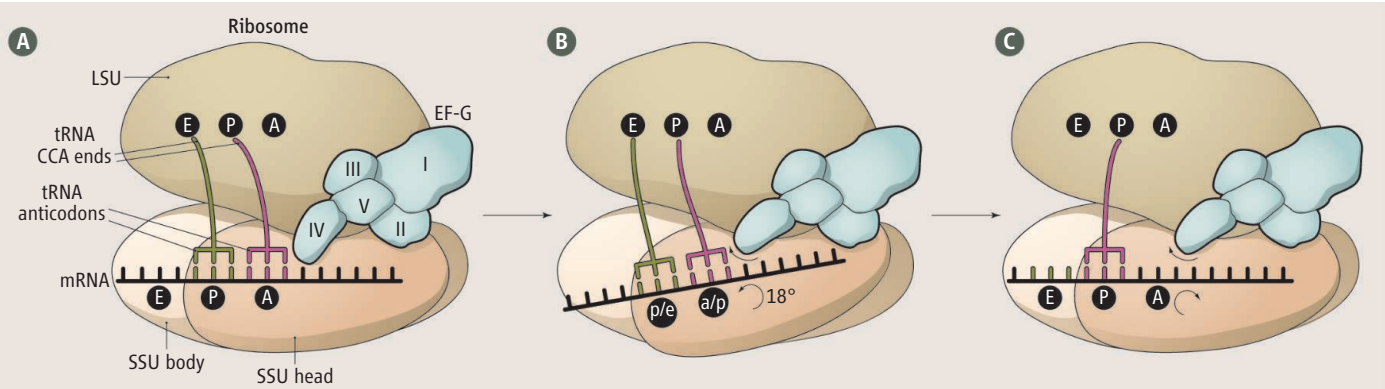

Translocation dynamics. (**A**) In the pretranslocation state of the ribosome, the tRNA anticodons are located in the A and P sites on the SSU, while the tRNA CCA ends oscillate between the A and P or P and E sites on the LSU. EF-G is in the GTP-bound conformation. (**B**) In the intermediate state of translocation, derived from the new crystal structures (*1*–*3*), the rotation of the SSU head domain brings the tRNA anticodons and the mRNA codons into a state intermediate between A and P (called a/p) or between P and E (p/e) on the SSU. Domain IV of EF-G moves. (**C**) In the posttranslocation state (*4*, *14*), only one tRNA is bound to the ribosome in the P site, the E-site tRNA is released, the SSU head domain is rotated backward, and EF-G has changed the conformation further before it dissociates from the ribosome (*1*–*3*).

of movement, and the new structures suggest how this is achieved. EF-G domain IV, which is essential for tRNA and mRNA translocation (*10*, *11*), projects into the A site, thereby preventing the backward movement of the tRNA (*1*–*3*) (see the figure, panel C). In addition, elements of 16*S* ribosomal RNA in the SSU act as molecular pawls to fix the position of the mRNA, preventing backward movement of the mRNA (*3*).

The structures also show how GTP hydrolysis in EF-G may be activated by the ribosome. In the structures by Tourigny *et al*. (*1*) and Pulk and Cate (*2*), the conserved histidine residue from switch 2 is poised for hydrolysis. By contrast, in the structure by Zhou *et al*. (*3*), this histidine is too far from the γ-phosphate to act in catalysis, suggesting that a nonactivated intermediate was trapped. Mutations of the histidine residue in either EF-G or EF-Tu, another translational GTPase, abolish GTP hydrolysis and block the progression through the translation elongation cycle (*9*, *12*), consistent with a catalytic role of the histidine. Key residues in EF-G and EF-Tu (*13*) form a nearly identical catalytic site, suggesting a common mechanism for the activation of translational GTPases by the ribosome.

The mechanism of translocation represents a case study of directed movement in large molecular machines. The new structures (*1*–*3*) suggest how GTP hydrolysis is coupled to translocation. The mechanism of coupling is reminiscent of motor proteins using ATP hydrolysis to drive directed movements (*2*). A remaining challenge is to determine the structure of a true pretranslocation complex (with tRNAs bound to both P and A sites and without EF-G occupying the A site of the SSU) and of intermediate states of translocation. Another key question is how EF-G accelerates translocation. Answering this question will require comparison of intermediate states of EF-G–catalyzed and spontaneous translocation.

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PLANETARY SCIENCE

Solving the Mascon Mystery

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Modeling the formation of regions of mass concentration may lead to new estimates of early heat flux in the Moon.

When we look at the Moon, we can see images of a man, a rabbit, and countless other analogies. These images are the figments of our imagination, inspired by the distribution of thick lava sequences, the mare basalts, that fill ancient basins that formed by large meteorite impacts early in solar system history. Still, mysteries remain hidden beneath the lunar surface. The first spacecraft in orbit around the Moon felt a stronger pull of gravity when passing over these basins, implying that a mass concentration, or "mascon," was present there (*1*). Subsequent studies added to the puzzle of mascons and provided partial explanations for their formation (*2*–*4*). On page 1552 of this issue, 45 years after the initial discovery, Melosh *et al*. (*5*) put all the pieces together and provide the first self-consistent model for the origin of mascons.

At first sight, the existence of mascons seems incompatible with the origin of the lunar basins in which they form. The impact process excavates a hole in the lunar crust and upper mantle, resulting in a mass deficit, not a mass concentration. The lunar mantle flows toward the basin interior and reduces the initial mass deficit. However, this flow process, which is similar to the rebound of

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