Concerning plate boundary geodynamics and tsunami hazard, an important question is whether Tohoku-type large shallow slip occurs commonly. The results of Chester *et al*. suggest that the shallow megathrust at the Japan Trench has special traits not seen in many other subduction zones. Ujiie *et al*. show that, because of lower clay contents, the fault zone material in the Nankai Trough in southwest Japan is not as weak as that in the Japan Trench.

The JFAST data show how direct borehole sampling and monitoring can help to elucidate the slip behavior of the shallow megathrust. Results from other ongoing and future megathrust drilling projects, such as those at Nankai and off Costa Rica, will enable comparisons between different subduction zones. However, while studying the shallow part of the fault, scientists must keep in mind that subduction earthquakes may generate devastating tsunamis even without huge shallow slip as in Tohoku, such as in Sumatra in 2004 and Chile in 2010.

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BOTANY

Shining Light at Microtubule Crossroads

Severing at microtubule crossovers reorients the plant microtubule network and redirects plant growth in response to light.

Antonina Roll-Mecak

The microtubule cytoskeleton, the network of cable-like tubulin polymers found throughout the cytoplasm in all eukaryotic cells, is central to cell division and differentiation throughout biology. Nowhere is this more true than in the plant kingdom. Here, microtubule organization patterns the deposition of cellulose, the prime constituent of cell walls, thus controlling the ability of plants to grow in the direction of light, or phototropism. The research article by Lindeboom *et al*. on page 1202 of this issue (*1*), together with several recently published studies (*2*, *3*), provides fundamental insights into the mechanism used by plants to switch the orientation of their cortical microtubule array, and therefore the morphology and function of the cells that harbor them, in response to light.

During cell elongation, cortical microtubules, those on the inner face of the plasma membrane, in the *Arabidopsis* hypocotyl (the stem of a germinating seedling) are arranged in parallel arrays with a predominant orientation almost perpendicular to the axis of expansion of the stem (see the figure, panel B, left). In response to light, microtubules undergo a rapid 90° reorientation, so they are now parallel to the stem, thereby changing the cellulose deposition pattern that controls cellular elongation. In an imaging tour de force, Lindeboom *et al*. now show that this reorientation of the microtubule array proceeds through two phases. The first phase involves γ-tubulin–dependent nucleation of new microtubules at angles ~40° from the existing transverse microtubules, thus generating crossovers. The second involves microtubule number amplification through severing at these microtubule crossovers (see the figure, panel B, center). Microtubule crossovers were previously shown to be hotspots for severing in cortical arrays (*4*). The new microtubule end generated by severing grows at a shallow angle, maintaining the overall orientation of the longitudinal "seed" microtubule, and thereby serves not only to amplify the number of microtubules but also to maintain the general orientation of the seed. This bifurcation of the microtubule by severing and regrowth is reminiscent of a railroad turntable where the subunits of the incoming train are separated from each other and then allowed to progress at different angles (see the figure).

The key player in this process is the microtubule-severing enzyme katanin, an AAA adenosine triphosphatase (ATPase) that is thought, by analogy with its family member spastin, to sever the microtubule through extraction of tubulin subunits from the microtubule lattice (*5*, *6*). Lindeboom *et al*. show that green fluorescent protein–labeled katanin is recruited to microtubule crossovers and that this recruitment precedes the formation of new microtubule plus ends (the growing ends of microtubules). A katanin null mutant shows no creation of new microtubule plus ends, as well as impaired reorientation of the array upon exposure to light. Because some of the new ends created by severing the microtubules do not depolymerize but are stable and able to regrow, severing has an overall constructive rather than destructive role and contributes to the net growth of the microtubule array.

One implication of this crossover-activated severing mechanism is that as the array gradually reorients and the population of longitudinal microtubules increases, the frequency of severing decreases (because there are fewer crossovers), thus dampening new microtubule generation and stabilizing the array in its new orientation. Interestingly, a complementary study by Zhang *et al*. (*2*), which makes similar observations, proposes that the dominant outcome of severing in the transverse hypocotyl microtubule array is depolymerization, with severing ultimately serving to eliminate unaligned, discordant cortical microtubules. Future studies will likely address the relative contributions of these two outcomes to overall array reorientation.

How does katanin distinguish crossover sites from bundled or single microtubules? A central question in cell biology concerns

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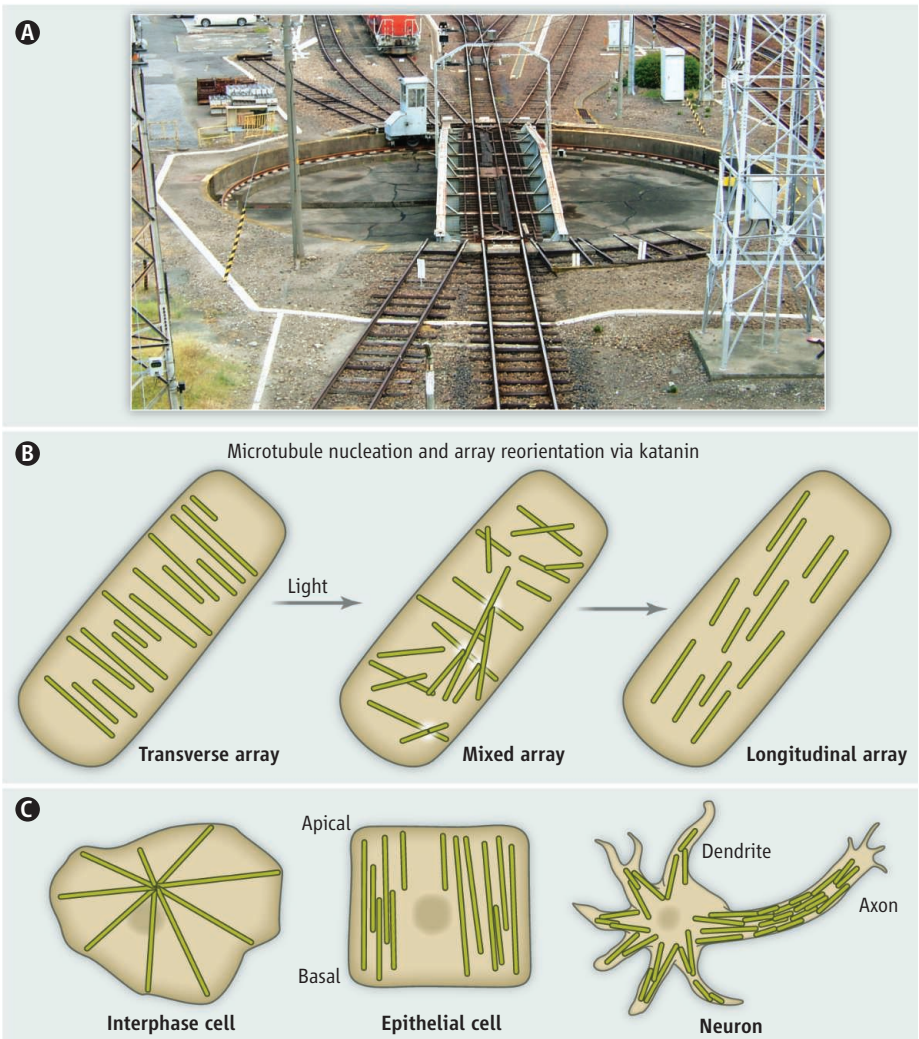

Making and remodeling microtubule arrays. (**A**) Severing dependent microtubule growth is analogous to a railroad turntable that splits two tracks. (**B**) Microtubule amplification and array reorientation are driven by katanin severing in the stem of a growing plant. (**C**) Microtubules are arranged in diverse patterns best adapted to cell type and organism: interphase cell, radial; epithelial cell, parallel; neuron, tiled.

the means by which nanometer-scale proteins sense and respond to cellular architecture at the micrometer scale. In vitro, katanin severs microtubules at any point along their length (*7*); however, experiments with dynamic microtubules or complex microtubule geometries more closely resembling those in cells have not been performed, and the fate of the new microtubule end generated by a microtubule-severing enzyme in vitro is still not known (does it catastrophically depolymerize, or is it able to regrow?). Katanin consists of a catalytic subunit (p60), which hydrolyzes ATP to locally disassemble the microtubule, and a regulatory subunit (p80) that enhances severing activity and targets the enzyme to specific subcellular locations (*6*). Katanin assembles into a hexamer with multiple microtubule-binding domains that could be maximally engaged only when two microtubules cross each other (*5*, *6*). It is also possible that the regulatory subunit, of which *Arabidopsis* encodes four, senses microtubule crossovers. Future studies will address whether p60 targeting to crossovers is impaired in p80 mutants.

Additional factors could also sense the microtubule crossover and regulate katanin function. A recent study in *Arabidopsis* pavement and petiole cells revealed that severing frequency at microtubule crossovers inversely correlates with the presence of the microtubule-associated protein SPIRAL2, which itself induces microtubule crossovers (*3*). The phenotypes of katanin and spiral2 mutants are diametrically opposed. The katanin mutant displays complex crossovers formed by multiple microtubules, whereas the spiral2 mutant has very few. How SPIRAL2 itself senses crossovers is not clear, but it might be transported along the microtubule to crossover sites (*3*). Last, katanin activity is sensitive to tubulin posttranslational modifications that could chemically mark microtubule crossover sites for severing action (*8*). Future in vitro studies with microtubule arrays of diverse geometries and in the presence of various microtubule-associated proteins will be essential in understanding the feedback between array architecture and katanin function.

A severing-dependent mechanism for microtubule amplification and array reorientation has been postulated to be important not only in the morphogenesis of noncentrosomal plant cortical arrays (*9*), but also in mitotic and meiotic spindles, epithelial cells, and neurons (*10*–*13*); however, it has not been directly observed in vivo until now, partly because the high microtubule density in these systems had impeded direct observation of severing. Centrosomes act as microtubule-organizing centers in animals; however, they pattern microtubules in an isotropic or radial array. Most cells in our body do not have radial microtubule arrays; many cells lack centrosomes altogether (*12*). Furthermore, the majority of microtubules in neurons or epithelial cells are disconnected from the centrosome (see the figure, panel C). Microtubule number amplification by severing is an attractive mechanism for generating the microtubule mass needed to fill long neuronal processes and offers the possibility of fast reorientation of the microtubule array in response to local stimuli. Thus, the mechanistic insights from the studies by Lindeboom *et al*. and Zhang *et al*. are likely to be relevant in other systems and firmly establish microtubule severing by katanin as a driving force in the making and remodeling of noncentrosomal ordered microtubule arrays.

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