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Myosin-driven transport network in plants is functionally robust and distinctive

Vitaly Citovsky^{a,1} and Bo Liu^b

Transport of Myosin Cargoes in Animal and Yeast Cells

Directional transport of intracellular cargoes by cytoskeleton-based motors is one of the signature features of eukaryotic cells. It was proposed that the last common ancestor of eukaryotes possessed several prototype motor proteins, including evolutionarily related kinesins and myosins (1, 2). Among these, there was an ancient myosin lineage that includes extant class V myosins conserved in animals, fungi, and Amoebozoa, and closely related class XI myosins conserved in green algae and plants (3, 4). Together with other recent studies, the paper by Kurth et al. in PNAS (5) uncovers a brand new mechanism underlying intracellular transport of myosin cargoes. Most importantly, the Kurth et al. paper shows that the green branch of the tree of life has evolved a very dense and largely unique endomembrane transport network empowered by myosins XI.

It is well recognized that long-range cargo transport is actin-centric in fungal and plant cells but mostly relies on microtubule-based motors in vertebrates (6, 7). The transport systems based on myosins V and XI exhibit remarkable variability in their functions and molecular organization in fungi and plants, respectively. First of all, myosin XI motors have much higher velocities, often greater than one order-of-magnitude faster, than myosin V (8). Most of what is known on myosin V-driven transport in the budding yeast *Saccharomyces cerevisiae* has to do with the delivery of secretory vesicles and organelles to a growing bud of the daughter cell (6, 9). On the other hand, plants harness both diffuse and polar cell growth mechanisms and exhibit vigorous intracellular dynamics in their fully expanded cells (10). Despite these differences, it seems instructive to compare the myosin V-dependent transport of secretory vesicles in yeast to the myosin XI-dependent transport of endomembrane vesicles in plants based on the novel data and concepts presented by Kurth et al. (5).

In budding yeast, the myosin V Myo2p, is recruited to the late Golgi and *trans*-Golgi network membranes via formation of a multisubunit complex that is attached

to or embedded in the membrane and is required for vesicle docking to and fusion with the exocyst (6, 11). This complex includes a pair of small Rab GTPases Ypt31 and Ypt32, and Sec2, a guanine nucleotide-exchange factor for Sec 4 (6). The latter is also recruited to this myosin receptor complex later in the transport process. A following modification of this complex, along with vesicle transport and a secretion process, involves Sec15, a Sec 4 effector that replaces Ypt31/32 before Myo2p and another myosin V, Myo4p, also transport organelles to the bud by using organelle-specific receptors and adaptors, including some Rab GTPases (9). The organelle transport in vertebrates shows some of the similar tendencies, including organelle-specific receptors (e.g., melanophilin) and Rab GTPases (6).

Transport of Myosin Cargoes in Plant Cells

The picture of the myosin XI-driven plant transport network painted by Kurth et al. (5) looks dramatically different. In contrast to yeast and vertebrates that possess two to three myosins V, flowering plants use a dozen or so of myosins XI that belong to five evolutionary lineages conserved throughout angiosperms, both monocots and dicots (12). A second principal component of the network is the MyoB family of myosin receptors; there are 16 of those in the model plant *Arabidopsis thaliana*. MyoBs are transmembrane proteins that directly bind to myosins and recruit these motors to vesicle-like endomembrane compartments that rapidly move along the F-actin tracks (5, 13). Surprisingly, none of the six MyoBs studied so far is colocalized with larger organelles, such as Golgi, peroxisomes, or mitochondria. Instead, the motile myosin XI-MyoB compartments drive cytoplasmic streaming that appears to carry passively moving organelles, secretory vesicles, and an inert tracer of the streaming (14).

Thus, a default model of the myosin transport in plants based on the data discussed above is dramatically different from what is known in yeast and vertebrates. In this model, the myosin XI-MyoB compartments represent a specialized transport system that drives streaming, rather than directly engaging individual organelles and secretory vesicles, which in

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turn delivers organelles and other types of vesicles to their destinations throughout the cell (14). Furthermore, existing genetic evidence indicates that cytoplasmic streaming is required for both polarized and diffuse cell growth because: (i) inactivation of myosins alone results in reduced cell elongation and expansion and affects plant growth and morphogenesis (15–20); (ii) simultaneous inactivation of myosins and MyoBs results in synergistic phenotypes (13, 14); and (iii) reduction in streaming velocity reduces plant growth, whereas increased velocity boosts that growth (21).

In addition to providing a deeper insight into the myosin-MyoB transport network, Kurth et al. used extensive yeast two-hybrid screens to discover two families of myosin adaptors termed MadA and MadB, which are conserved in plants (5). These newly identified proteins, unrelated to each other or to MyoB, bind to myosins directly and are typically localized to vesicle-like membranes despite lacking detectable transmembrane α -helices.

Another interesting outcome of the work is an expansion of the myosin transport network into the nucleus. Kurth et al. (5) raise two possibilities as to how myosin transport may be involved in nuclear dynamics and nucleocytoplasmic transport, even though the presented data are far from conclusive. Confocal images led to a hypothesis that linear arrays of the myosin-transported cargo cross the nucleus resembling transvacuolar strands, perhaps moving along the F-actin-containing cytosolic sleeves (5), which awaits confirmation by electron microscopy and genetic analyses. It is intriguing that one of the newly discovered myosin adaptors, MadA1, is localized to the nucleus and appears to be pulled out of the nuclear interior in rapidly moving particle arrays (5). Perhaps an active, myosin-dependent nuclear export could be proposed when functional colocalization of myosin XI and MadA1 is demonstrated and hypothetical MadA1-containing complexes are characterized.

With multiple homologous proteins in hand, Kurth et al. (5) took one step further to analyze the protein interaction network composed of myosins XI and their protein partners, including MyoB receptors, MadA and MadB adaptors, and a few other myosin-interacting proteins (5). It was found that this network is dense and highly interconnected with significant prevalence of myosins and MyoBs, and that each interact with multiple partners. Only a few “specialists” in this network—including a previously described, outer nuclear receptor of myosin XI-I, WIT2 (22)—were found. Such network structure clearly attests to the functional robustness of myosin-directed transport pathways in plants, in full accord with genetic analyses showing partial functional redundancy of myosins (18), MyoBs (13, 14), and MadB adaptors (5).

Kurth et al. (5) also take an evolutionary view of the plant myosin transport network and conclude that it is of ancient origin, likely dating back to a common ancestor of green algae and land plants. That prototype network perhaps included myosins XI, as well as MadA and MadB adaptors (5). It is proposed that MyoB receptors that dominate the extant network evolved later, in a freshwater Characean algal lineage that is ancestral to land plants. Moreover, it is suggested that the dramatic expansion of the myosins XI, MyoB, MadA, and MadB families in Angiosperms likely have contributed to a remarkable success of flowering plants

in diversifying, colonizing the land, and enabling the existence of the biosphere in which we all live.

Future Directions

As is typical of works of significant impact, Kurth et al. (5) pose a series of unanswered questions that will drive exciting future research. One most pressing question concerns molecular composition and biogenesis of the vesicle compartments defined by the MyoB,

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MadA, and MadB proteins. In particular, are there specific cargoes in each of these compartments, or do they function solely to establish cytoplasmic streaming patterns that carry the secretory vesicles and organelles? What are the relative contributions of these compartments in cytoplasmic streaming?

Another question is whether the streaming network is organized to direct cargoes to their proper destinations in a cell type-specific manner or if it works simply to intermix the cytosol, with cargoes being docked to their respective destination sites. Are MadA and MadB proteins incorporated into MyoB-containing receptor complexes, or do they define distinct vesicular compartments? It becomes particularly intriguing to learn the functions of distinct pathways defined by subfamilies of MyoB receptors or by MadA and MadB adaptors because Kurth et al. provide the first insight into the function of the MadB proteins in polarized growth of root hairs (5).

In conclusion, what has emerged from the Kurth et al. (5) paper is an extremely rich, colorful, and original picture of a myosin-dependent transport system in plants that is characterized by evolutionary inventions, and plays critical roles in vigorous, high-velocity cytoplasmic streaming, cell expansion, and plant development (5). Because of the functional and evolutionary significance of the myosin-driven transport, an immediate impact on the broad field of plant cell biology is expected. But what is in it for those working beyond this field? An immediate simple answer is that we all should care for the workings of the plant cell because plants sustain life on Earth. Furthermore, understanding how the myosin transport network drives cell growth and plant development is critical for engineering crops to meet the need of a growing human population. Finally, with the advent of synthetic biology, we could imagine engineering organisms tailored to harness the most powerful cellular systems from diverse sources. The myosin-driven transport system in plants undoubtedly is a good candidate.

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