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# Dyneins Have Run Their Course in Plant Lineage

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**Flowering plant genomes lack flagellar and cytoplasmic dyneins as well as the proteins that make up the dynactin complex. The mechanisms for organizing the Golgi apparatus, establishing spindle poles, and moving nuclei, vesicles, and chromosomes in flowering plants must be fundamentally different from those in other systems where these processes are dependent upon dynein and dynactin.**

**Key words: dynein, dynactin, cytoskeleton, motor protein, angiosperm, evolution**

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One of the major effects of large-scale sequencing and rapid computer-based sequence comparisons has been the recognition that many proteins are evolutionarily conserved among eukaryotes. This seems to be particularly true for proteins involved in intracellular motility. For instance, the cytoskeletal proteins tubulin, actin, myosin, and plus and minus end-directed kinesins are ubiquitous in fungi, animals and plants. We were therefore surprised to find that the genes for cytoplasmic dynein and its partner dynactin, although present in fungi and animals, were not identifiable in higher plant expressed sequence tag (EST) databases or the sequence of the recently published *Arabidopsis* genome (1).

Cytoplasmic dynein is a large protein complex that acts as a microtubule-dependent, minus end-directed motor. It is required for intraflagellar transport (IFT), is involved in organizing the Golgi apparatus and spindle poles, and has roles in moving nuclei, vesicles, pigment granules, and chromosomes (2, 3). Dynein is composed of heavy chains, intermediate chains, a family of light intermediate chains, and several different light chains. It is activated by dynactin, another large protein complex that is believed to couple dynein to its cargoes. Ten genes encode the subunits of the dynactin complex: p24, p25, p27, p32, p37, p62, Arp1, Arp11, dynamitin, and p150$^{Glued}$. We found that of all the dynein and dynactin subunits, only dynein light chain LC8, which interacts with a number of unrelated enzymes (2), is represented in the angiosperm sequences present in GenBank.

A variety of data suggest that cytoplasmic dynein is also present in protists and lower plants, and that at least a subset of the known dynein functions are conserved in these organisms. It is known, for instance, that cytoplasmic dynein is involved in organelle transport in the protist *Dictyostelium* (4). In all land plants except angiosperms (flowering plants), a flagellar apparatus is present during some stage of the life cycle. The microtubules of their flagella are typically arranged (in a $9+2$ pattern), with inner arm dyneins present (5). This implies that the motors that facilitate anterograde and retrograde IFT, namely kinesin-II and cytoplasmic dynein, are functioning in the flagella of these plants. The striking absence of sequences homologous to kinesin-II, cytoplasmic dynein, and flagellar dynein in angiosperms suggests that these genes and their respective functions may have been lost in angiosperms concomitant with the loss of the flagellar apparatus.

Without components of cytoplasmic dynein and dynactin, angiosperms manage to organize the Golgi apparatus and move nuclei and vesicles efficiently. Perhaps of greater significance is the fact that angiosperms form spindles and carry out orderly chromosome segregation in the absence of cytoplasmic dynein. Although it is clear that plants possess homologs of many animal/fungal proteins involved in chromosome movement and spindle assembly (6), the mechanisms of plant cell division must in some ways be quite different from those of animals and fungi. One area where the absence of dynein may have a major effect is at the spindle poles. In animals, dynein and the associated protein NUMA are required to organize the typically focussed spindle poles (7), while in plants both proteins are absent and the spindle poles are diffuse and unfocussed (8). Since cytoplasmic dynein and dynactin are required for the normal growth and development of fungi and insects, they may be useful targets for the development of argicultural fungicides and insecticides.

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