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Hepler P K & Palevitz B A. Microtubules and microfilaments.  
*Annu. Rev. Plant Physiol.* 25:309-62, 1974.  
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The literature on microtubules and microfilaments is reviewed, with emphasis placed on motility and morphogenesis in plants. New information is reported on the presence of actin in streaming cells and on the determination of the division plane in plants. Hypotheses are developed that attempt to explain the role of cortical microtubules in the orientation control of cellulose microfibrils and the significance of the structural interaction between membranes and microtubules in the mitotic apparatus. [The SCI® indicates that this paper has been cited in over 285 publications.]

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The answer to the question, "Why did we write the review on microtubules and microfilaments?" is simple: one of us (PKH) was asked. The task, however, was not simple. Microtubules had been reviewed authoritatively five years earlier by Eldon Newcomb<sup>1</sup> but had grown rapidly since that time; furthermore, a second major subject, namely, microfilaments, was to be covered as well. I was both excited and apprehensive about my ability to pull these subjects together. I was, however, fortunate in having in my laboratory Barry Palevitz, an able and enthusiastic postdoctoral fellow, whose help I quickly enlisted. We easily divided the task; Barry would cover microfilaments, and I would tackle microtubules.

The early 1970s were exciting times in the areas of cell motility and the cytoskeleton. In preparing the review, however, we found that the amount of work on microtubules and microfilaments and their constituent proteins in plants was quite limited. Although some important initial discoveries had been made from studies of plant cells, as interest in the cytoskeleton grew the emphasis had quickly shifted to studies on animal-cell systems. We became quite aware of major gaps in our knowledge of motility in plant cells as the review

took shape and to a certain extent used our task as a springboard for some of our own work, especially on microfilaments.

Microfilaments had been suspected of being composed of actin; however, definitive proof was lacking. Barry proposed examining microfilament bundles in the green alga *Nitella* to see if they would react with skeletal-muscle heavy meromyosin. I thought that the experiment had probably already been tried by several other laboratories and that it had failed, since if it had succeeded surely it would have been published. Barry, however, proceeded with the study and quickly showed that extruded microfilaments from *Nitella* bound heavy meromyosin with the characteristic arrowhead pattern, diagnostic for actin. Although these studies were published separately a few months before the review appeared,<sup>2</sup> we think that inclusion of these studies in the review added a sense of excitement and progress to the topic of microfilaments in plants.

There were other areas in the review where we strove to introduce new thoughts and promising avenues for future research, including spindle rotation and the mechanism of division plane determination in plants<sup>3</sup> (a topic that Barry still pursues). Also, we developed a model in which we suggested that, through the action of mechanochemical cross-linkers, microtubules might cause a directed flow of macromolecular assemblies in the plane of the plasma membrane that orients the growing cellulose fibril. Finally, we explored, for the first time, the meaning of the structural interrelationships between microtubules and endomembranes in dividing cells and suggested that these membranes control the calcium ion concentration and thus possibly the formation and function of the mitotic apparatus. These last thoughts have dominated my research ever since.

I became aware that the review was being read widely one summer (1979) while working in the library at the Marine Biological Laboratory. I turned to the library's volume of the *Annual Review of Plant Physiology* that contained our paper and when I put the volume down, it literally fell open at our article; worn edges on the pages and the penciled corrections of all the misspellings and punctuation errors indicated that the chapter had been thoroughly perused. Several reasons account for its frequent citation. The review appeared at a time when interest in the plant cytoskeleton began to increase sharply. The breadth of the review also drew interest from nonbotanists, since we had covered in detail work on animal as well as plant microtubules and microfilaments. Finally, we would like to think that the infusion of our own original work and thinking captured the interest of scientists publishing in the area of the cytoskeleton.

For a recent review, see reference 4.

1. Newcomb E H. Plant microtubules. *Annu. Rev. Plant Physiol.* 20:253-88, 1969. [See also: Newcomb E H. Citation Classic. *Current Contents/Agriculture, Biology & Environmental Sciences* 11(6):16, 11 February 1980.]
2. Palevitz B A & Hepler P K. Actin in the green alga, *Nitella*. *Proc. Nat. Acad. Sci. US* 71:363-6, 1974. (Cited 85 times.)
3. -----, The control of the plane of division during stomatal differentiation in *Allium*. I. Spindle reorientation. *Chromosoma* 46:297-326, 1974.
4. Gunning B E S & Hardham A R. Microtubules. *Annu. Rev. Plant Physiol.* 33:651-98, 1982.