This Week's Citation Classic

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The review emphasizes that microtubules occur generally in plant cells and participate in a variety of subcellular structures and functions. Considerable evidence suggests that cortical microtubules may control the orientation of cellulose microfibrils as the latter are being deposited in the cell wall. [The $SC/^{\odot}$ indicates that this paper has been cited over 150 times since 1969.]

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"This review resulted from my long-term interest in the way in which the cytoplasm controls the structure of the plant cell wall during growth and differentiation. In the late 1950s Kenneth Siegesmund and I attempted rather unsuccessfully to study this problem by looking for changes in the ultrastructure of the wall and adjacent cytoplasm in enlarging tobacco pith cells fixed in permanganate. In the early 1960s Peter Hepler, a young graduate student, started working with me on the problem. As experimental material we used cultured internodes excised from Coleus stems. When the stem internode is notched so as to sever a vascular bundle, parenchyma cells interior to the cut reestablish the xylem pathway by differentiating into tracheary elements. During differentiation these cells deposit thick bands of secondary wall composed of cellulose microfibrils. We reasoned that we might be able to detect changes in the cytoplasm underlying the development of these wall thickenings, possibly even including the appearance of an element that could control the orientation of the microfibrils during their deposition.

"After using permanganate for a time without success, Peter adopted glutaraldehyde fixation following the appearance of the landmark work of Sabatini, Bensch, and Barrnett in 1963.¹ Shortly thereafter he discovered that microtubule-like elements occur in the cytoplasm immediately beneath the secondary wall bands and parallel the band microfibrils in orientation. Later in 1963 I left Madison to spend a year in K. R. Porter's laboratory at Harvard, taking with me the manuscript of a short paper describing our results. I produced this at my first conference with Porter. I was shocked when he showed me a far more thorough study establishing microtubules as elements of plant cell structure, which Ledbetter and he had already submitted for publication.²

"At Harvard I became acquainted with Howard Bonnett, who in 1964 was completing his PhD degree in plant physiology. Howard came to Madison on a postdoctoral fellowship, and we spent the next two years exploring coated vesicles, protein accumulations in ER cisternae, and other interesting ultrastructural features of root hairs. As for microtubles, a peculiarity of root hair wall structure permitted a highly suggestive correlation to be made. Howard showed that at the growing tip, where the microfibrils are deposited randomly, there are no microtubules, but along the nongrowing sides of the hairs, where microfibrils are deposited axially as a sort of secondary wall, there are microtubules in the adjacent cytoplasm, and they run axially. A study of the relationship of microtubules to cell plate formation in dividing cells resulted from Peter Hepler's return to my laboratory for a few months in 1966 following army service.³

"I think this article has been cited frequently because it was the first review to appear in the plant literature on a subject that has continued to increase in importance and general interest, and it examines in detail the evidence correlating the orientation of cortical microtubules with that of newly deposited wall microfibrils. The subject was reviewed again in the same series by Hepler and Palevitz in 1974."⁴

- 1. Sabatini D D, Bensch K & Barmett R J. Cytochemistry and electron microscopy. J.Cell Biol. 17:19-34, 1963.
- Ledbetter M C & Porter K R. A "microtubule" in plant cell fine structure. J. Cell Biol. 19:239-50, 1963.
 Hepler P K & Newcomb E H. Fine structure of cell plate formation in the apical meristem of
- Phaseolus roots. J. Utrastruct. Res. 19:498-513, 1967.
- Hepler P K & Palevitz B A. Microtubules and microfilaments. Annu. Rev. Plant Physiol. 25:309-62, 1974.