

# This Week's Citation Classic™

CC/NUMBER 13  
APRIL 1, 1985

**Mühlethaler K.** Ultrastructure and formation of plant cell walls.

*Annu. Rev. Plant Physiol.* 18:1-24, 1967.

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In this paper, various concepts of the fibrillar structure of cellulose are reviewed and a new hypothesis for cell-wall deposition involving Golgi-derived vacuoles and plasmalemma-bound particles is presented. [The SC]<sup>®</sup> indicates that this paper has been cited in over 130 publications since 1967.]

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February 12, 1985

Before the introduction of the electron microscope (EM), the ultrastructure of cell walls was studied by indirect methods, such as polarized light and X-ray diffraction analysis. Using these methods, it was only possible to determine the coarse orientation of cellulose molecules and their accompanying matrix constituents, such as hemicellulose, lignin, and pectin. With the introduction of EM, I hoped to directly visualize these high-molecular weight components and to obtain an insight into the dynamic aspects of the cell wall, such as its growth and differentiation.

In contrast to the delicate protein structure of the cytoplasm, the cell walls represented a more resistant object for EM studies. One major problem was dissecting them thin enough to allow an optimal penetration of the electrons. In the absence of a suitable thin-sectioning technique, we tried to disperse the walls using ultrasonification, by degradation with lytic enzymes, or by filling a bullet with them and shooting it against a steel plate. In spite of all these efforts, the results were not rewarding. In 1967, when this paper was

published, the methodology was far advanced, including techniques for sectioning, shadowing, negative staining, and freeze-etching. The last method had been developed a short time before in our laboratory.<sup>1</sup> In addition, the X-ray diffraction analysis, which allowed conclusions on stereochemical aspects, interatomic bond distances, and the orientation of the molecular chains in the crystalline state, furnished new data concerning the arrangement of different substances present in the cell wall. In combining the results with various EM observations, a new concept of cellulose structure, beginning with its molecular chains and going up to the fibrillar strands, could be postulated.

Based on observations obtained by freeze-etching, which allowed us to observe large areas of the cell surface at various stages of wall formation, I came to the conclusion that two processes are involved in its deposition. First, matrix substances, such as pectin, are moved to the cell surface by Golgi-derived vacuoles and, simultaneously, the membrane-bound particles seem to be involved in the mechanism of cellulose strand formation. At first these fibrils are deposited at random in a loose network. Then, as the wall thickens, these fibrils are laid down in parallel, oriented, dense sheets. At the time this paper appeared, it met with some scepticism because the concept of the chain model of cellulose fibrils was new. In addition, our EM observations indicated that the plasmalemma particles seemed to be involved in cell-wall formation, which was unorthodox. Today, this concept has been confirmed and is presented in textbooks.<sup>2</sup> At the time this paper was published, new discoveries in cell biology were frequent and easy to make because the new methods developed in cell and molecular biology were paying their dividends.

1. Moor H, Mühlethaler K, Waldner H & Frey-Wyssling A. A new freezing-ultramicrotome. *J. Biophys. Biochem. Cytol.* 10:1-13, 1961. (Cited 355 times.)
2. Robinson D G. *Plant membranes*. New York: Wiley, 1985. 1075 p.