## This Week's Citation Classic 2

Roelofsen P A & Houwink A L. Architecture and growth of the primary cell wall in some plant hairs and in the Phycomyces sporangiophore. *Acta Bot. Neer.* 2:218-25, 1953. [Laboratory of Technical Botany and Technical Physics Department, Delft University of Technology, The Netherlands]

Cellulose, in the form of microfibrils in cell walls of plants, is the most abundant macromolecule on Earth. The important contribution of P.A. Roelofsen in this field was that he made an attempt to develop a general theory, the multinet-growth hypothesis, to explain the cell wall texture in growing cells. [The SCI® indicates that this paper has been cited in more than 115 publications, making it the most-cited paper published in this journal.]

## The Multinet-Growth Hypothesis

M.M.A. Sassen
Department of Experimental Botany
University of Nijmegen
6525 ED Nijmegen
The Netherlands

As early as 1864, C.W. Naegeli, using a polarizing microscope, discovered that cellulose occurred in plant cells in the form of tiny crystals, which he called micellae. It was not until 1948, however, that the true shape of micellae could be made visible with the aid of the electron microscope. In that year, A. Frey-Wyssling and coworkers,2 for higher plants, and R.D. Preston and coworkers,3 for algae, discovered independently that the micellae described by Naegeli actually consisted of long, thin threads, with a diameter of 25-30 nanometers and an indeterminate length. These threads were called cellulose microfibrils (CMFs). From that day on, research has continued into the texture, i.e., the pattern of the CMFs in the cell walls of various cell types.

Until his untimely death in 1966, P.A. Roelofsen made important contributions to this research. He can be credited with being the first to describe systematically

the cell wall textures of various cell types.4 In addition, he successfully developed a general theory, the "multinet-growth" hypothesis (MGH), to explain the cell wall textures in growing cells. In the subject of this classic, Roelofsen and his coworker, A.L. Houwink, described what he had observed in the wall of growing cells. "The cellulose fibrils on the interior surface of the primary cell wall of growing hairs of Ceiba, Asclepias and Gossypium are oriented more or less transversely. In more peripheric layers their direction changes gradually until they are mainly axial in the outermost layer." He later expanded the theory to include other growing cells.5

From the start, his theory had its proponents as well as opponents, although no alternative explanation for the observed textures was proposed. At the same time, it remained a theory, since all that could be observed was the final result of a process; the intermediate steps had never been studied. Although different views on the textures in growing cell walls still exist,6 the MGH, on the whole, has been accepted and has found its way into all modern textbooks that discuss the cell wall. In recent years, the interest in cell wall research has increased greatly, and more and more examples of cell wall growth are being investigated. The reorientation of CMFs during cell wall growth is now also being studied quantitatively.7,8 This type of research has shown that the theory will have to be adapted slightly. Nevertheless, it may be said that Roelofsen's MGH has been a great stimulus to cell wall research and is still vielding new results.

Naegeli C W. Ueber den inneren Bau der vegetabilischen Zellmembranen. Sitzungsber. Bayer. Akad. Wiss. 1:282: 2:115, 1864.

Frey-Wyssling A, Mühlethaler K & Wyckoff R W G. Mikrofibrillenbau der planzliche Zellwände. Experientia 4:475-6, 1948. (Cited 75 times.)

Preston R D, Nicolai E, Reed R & Millard A. An electron microscope study of cellulose in the wall of Vallonia ventricosa. Nature 162:665-7, 1948.

<sup>4.</sup> Roelofsen P A. The plant cell wall. Berlin, FRG: Borntraeger, 1959. (Cited 125 times.)

Ultrastructure of the wall in growing cells and its relation to the direction of the growth.
 Advan. Botan. Res. 2:69-149, 1965. (Cited 80 times.)

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<sup>8.</sup> Sassen M M A & Wolters-Arts A M C. Cell wall texture and cortical microtubules in growing staminal hairs of Tradescantia virginiana. Acta Bot. Neer. 35:351-60; 1986.