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Darvill A G & Albersheim P. Phytoalexins and their elicitors—a defense against microbial infection in plants. *Annu. Rev. Plant Physiol.* **35**:243-75, 1984. [Depts. Chem. and Molecular, Cellular, and Develop. Biol., University of Colorado. Boulder, CO]

This review summarized the evidence supporting the hypothesis that accumulation of phytoalexins at the site of attempted infection is an important mechanism by which plants resist disease. This hypothesis has been strongly supported by evidence published after publication of the review. The molecules that signal plants to begin synthesizing phytoalexins are called elicitors, and the review emphasized the identification and characterization of the elicitors that are oligosaccharide constituents of the polysaccharide components of the cell walls of fungi and plants. [The SCI^{\varnothing} indicates that this paper has been cited in more than 325 publications.]

Studies of Phytoalexins and Their Elicitors Led to the Discovery of Oligosaccharins

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We wrote the review on phytoalexins and their elicitors at a very exciting time in our laboratory. In the several years preceding 1984 we had emphasized two independent projects in our research. One project studied the structures of plant primary cell wall polysaccharides and the other, how plants protect themselves from microbial invasion. At the time the review was published, we had just come to the realization that these two research projects showed considerable overlap. It was in this review that we first put forward the hypothesis that the cell walls of plants contain oligosaccharides that can function as regulatory molecules. This field has since expanded into a major area of plant research, and such oligosaccharide regulatory moiecules are called "oligosaccharins.

In 1984, our structural studies on plant cell wall polysaccharides were beginning to indicate that the polysaccharides found in the cell wall (particularly the pectins and hemicelluoses) are very complex but definitely not random structures. We came to realize that the well-known structural role of these polysaccharides is not the driving force behind the evolutionary conserved structural complexity of these cell wall polymers. In our host-pathogen studies, we, with the extremely capable help of then graduate students Barbara Valent, Michael Hahn, and Janice Sharp, and research associate

Michael McNeil, had recognized that a structurally defined hepta-|3-glucoside in the cell wall of the fungus Phytophthora megasperma f.sp. glycinea is an elicitor of phytoalexins in soybean cotyledons. The hepta-p-glucoside elicitor was structurally characterized, and the structure confirmed by chemical synthesis. Other hepta-p-glucosides of very similar structure were shown to have no elicitor activity. These results provided the first compelling evidence that plants have the capacity to recognize structurally defined oligosaccharides as regulatory molecules. During our attempt to identify similar molecules in bacterial cell walls, we and Hahn realized that plant cell walls themselves contain an elicitor of phytoalexins. This pectic "endogenous elicitor" was shown to be a size-specific "DP 12-14" oligogalacturonide resulting from cleavage of cell wall homogalacturonan. As described in our 1984 review, this exciting observation suggested, for the first time, that plant cell wall polysaccharides contain oligosaccharides that, when released, can function as regulatory molecules.

Since the observations written in our 1984 review, the field of oligosaccharide regulatory molecules, "oligosaccharins," has grown considerably. Not only are oligosaccharides now recognized as important in host-pathogen interactions, they are also seen as key regulatory molecules in the control of plant growth and development.²³ The oligosaccharin field has also expanded to include lipo-oligosaccharides of bacterial origin that are key signal molecules in the development of the symbiotic relationship between Rhizobiaand legume hosts. These oligosaccharins have been called nod factors and are also capable of inducing organogenesis in plants. Indeed, it has been suggested that plants themselves contain related lipo-oligosaccharide regulatory molecules that function in normal growth and development.

We personally are very excited by the expansion of the oligosaccharin field that has occurred since we wrote the first review on this subject. The field is expanding to include studies of proteins involved in the release, processing, and perception of oligosaccharins. It is through the molecular biological control of these proteins that scientists are most likely to be able to control oligosaccharin activities and, in turn, to realize the goal of controlling plant growth, development, and the relationships of plants with microbes.

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