Peter Albersheim

Peter Albersheim made a big contribution to our understanding of plant cell wall structure and function, especially the role that complex carbohydrates, such as pectins and hemicelluloses, have on the modality of the cell wall. His laboratory was the first to show that carbohydrates, called oligosaccharins, have a regulatory function in plant cells. Peter had a unique ability to look outside the box, combine different branches of science, and innovate. He published over 300 papers and left a legacy to build upon. However, Peter would be the first to say that he walked on the footsteps of others, and with others, from whom he learned and whom he taught. He enjoyed challenging colleagues, students and postdocs to think with open minds from all possible angles. It was not unusual to see him walk the halls of his laboratories day and night, entering the labs to talk about projects with whomever happened to be there working on their experiments or getting ready for exams. He taught colleagues and students to stand on their feet and defend their results, ideas and hypotheses – important skills to have when they had to present their work at meetings and conferences.

How it all began

Peter was born on the 30th of March 1934 in New York City, NY. His parents, Walter and Alberta, already had a two-and-a-half-year-old daughter, Anne. Peter's father,

who emigrated from Germany in 1924, worked for Bell Labs. His job took the family first to Great Neck, Long Island, NY in 1937. The family moved again, after Japan attacked Pearl Harbor – this time to Interlaken, NJ in 1942. Peter's best childhood friend was James Carton. They met on the bus taking Peter to his first day in the new school in Interlaken. They bonded over their love for outdoors and became inseparable. They spent summer days fly fishing on Lake Deal and winter months trapping muskrats. They rode "their bikes for miles, in the cold bleakness of early mornings, in order to set traps before school" (Albersheim 2016). Peter's German shepherd, Ric, followed and protected them from older boys trying to steal their traps.

Peter went to a summer farming camp when he was ten years old. The time spent at camp had a profound influence on Peter and he dreamed of becoming a farmer. This childhood dream was a big part of Peter's decision, years later, to choose Cornell University School of Agriculture for his undergraduate studies. During the three summers while a student at Cornell, Peter worked as a helper on nearby farms. There, Peter witnessed the devastating effect plant pathogens had on crops as well as the economic and social impact on families owning these farms. A keen observer, Peter was intrigued by plants that stood out because of their resistance to disease. He wanted to learn and understand what it was that made these plants resistant while others around them succumbed to disease. Therefore, Peter decided to major in plant pathology.

Peter went to the Asbury Park High School, where he became aware of his love for science and teaching. He helped his friends study when they had a hard time understanding biology and chemistry, especially organic chemistry. Hence, Peter also took chemistry courses while majoring in plant pathology at Cornell. This background inspired him to enroll in a graduate program at the California Institute of Technology in September 1956. His PhD thesis advisor was Dr. James Bonner. In Bonner's lab Peter quickly discovered the joy of scientific research. From then on the drive to discover the unknown, the elation of overcoming the challenge of the experimental design, and the high of the scientific discovery, never left him.

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PETER ALBERSHEIM ***continued***

James Bonner introduced Peter to the chemistry of pectin, the polysaccharide made by plant cells as one of the building blocks of their cell walls. Peter's PhD thesis confirmed Dr. Bonner's hypothesis that auxin regulates the rate of plant growth, in part, by regulating methyl esterification of pectin (Sato et al. 1958; Albersheim and Bonner 1959; Jansen et al. 1960; Albersheim 1963b).

Peter stayed in Bonner's lab for three months after receiving his PhD, and discovered in the spring of 1959 that a viscous solution of citrus pectin lost its viscosity when boiled at pH 6.8 for 5 minutes. The loss of viscosity was caused by depolymerization of pectin. Peter spent the following year at the Swiss Federal Institute of Technology as a postdoctoral fellow. There he discovered an enzyme pectin transeliminase, now known as pectin lyase, that depolymerized pectin at pH 5, similar to the results obtained after boiling the pectin for 5 minutes at pH 6.8 (Albersheim et al. 1960; Albersheim and Killias 1962; Albersheim 1963a). The pectin lyase was isolated and purified from commercial citrus pectinase and was shown to break pectin by a b- elimination reaction resulting in the formation of unsaturated methyl oligogalacturonates with double bonds between C4 and C5 of the terminal galacturonosyl residues.

Starting his own laboratory

Peter, finishing his postdoctoral studies in Switzerland, returned to the US and became a Lecturer at Harvard University, Cambridge, MA. A year later, he was appointed an Assistant Professor. Peter stayed at Harvard for four years. He moved to the University of Colorado- Boulder in 1964 where he became a full Professor in 1967. He taught biology, biochemistry, as well as molecular, cellular and developmental biology. Peter thought of his lab as a family. He took his students, postdocs and visiting scientists skiing, hiking and fly fishing, thus introducing them to his own early passion for the outdoors.

Peter knew that in order to understand plant defense mechanisms against pathogens he needed to understand the structure and function of the plant's first layer of defense, the cell wall. His research at Harvard and the University of Colorado concentrated on the primary cell wall, the thin layer surrounding growing plant cells, primarily composed of complex carbohydrates.

About 70% of the carbohydrate content of primary cell walls are non cellulosic polysaccharides, pectin and hemicellulose. While the chemical structure of cellulose is relatively simple (it is an unbranched b-1,4 linked glucan with a disaccharide repeating unit), the structure of pectin and hemicellulose is far more complex. Although the plant cell wall polysaccharides are composed of only 13 different glycosyl residues many of them are structurally modified. This structural diversity contributes to the complexity of the cell wall structure.

Peter's lab contributed many methods to structurally characterize complex carbohydrates. The sugar composition analysis (Albersheim et al. 1967; Jones and Albersheim 1972) led the way to the development of methods for glycosyl linkage analysis (Talmadge et al. 1973; McNeil and Albersheim 1977; Valent et al. 1980; Darvill et al. 1980; Waeghe et al. 1983; Sharp and Albersheim 1984; McNeill et al. 1982a; Doares et al. 1991; Bauer et al. 1973). The first method to structurally characterize complex carbohydrates with repeating glycosyl residues, of up to seven residues, was developed by Dr. Bengt Lindberg and his colleagues in Stockholm, Sweden. Peter and his team were successful in modifying Lindberg's method and were able to structurally characterize carbohydrates with repeat units of up to 11 glycosyl residues.

The early plant cell wall extraction procedures from plant material were harsh and caused reduction in the degree of polymerization. Peter was able to obtain suspension-cultured sycamore cells from Dr. Derek Lamport of Cambridge University, UK. The suspension-cultured cells secrete cell wall polysaccharides into the culture medium, thus eliminating the need for extraction. Peter's lab started the work on characterizing the structure of plant cell wall polysaccharides using both extracellular polysaccharides and cell wall polysaccharides isolated from the cultured cells. Each student in

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the lab (Ken Keegstra, Dietz Bauer and Ken Talmadge) was assigned a particular polysaccharide to work on. Although cell wall polysaccharides were excreted into the medium by suspension cultured cells, the methods still had to be developed to separate different polysaccharides from each other. This collaborative work led to the characterization of plant cell wall hemicellulose xyloglucan (Bauer et al. 1973; Wilder and Albersheim 1973) as well as rhamnogalacturonan and homogalacturonan (Talmadge et al. 1973). As a result, Peter's lab published one of the first plant cell wall models in 1973 (Keegstra et al. 1973).

Hemicelluloses, like xyloglucan and glucuronoarabinoxylan (Darvill et al. 1980) that were later characterized from cultured plant cell walls in Peter's lab, have a backbone similar to cellulose. Because of that similarity in structure, xyloglucan and xylan bind to cellulose via hydrogen bonds (Bauer et al. 1973; Valent and Albersheim 1974; Pauly et al. 1999). Xyloglucan has side chains containing xylosyl, galactosyl, arabinosyl, and fucosyl residues (York et al. 1988; Kiefer et al. 1989; Kiefer et al. 1990; Hisamatsu et al. 1991; Hisamatsu et al. 1992; York et al. 1993; York et al. 1995; Pauly et al. 2001a; Pauly et al. 2001b; Jia et al. 2003; Freshour et al. 2003; Stevenson et al. 1986; Moore et al. 1986; York et al. 1990; Hantus et al. 1997; York et al. 1996).

Rhamnogalacturonan-I (RGI) is a family of large polysaccharides with a backbone of repeating disaccharide units -4)-a-D-GalAp-(1-2)-a-L-Rhap(1-. Half of the rhamnosyl residues are substituted at C4 with side chains containing L-arabinosyl, D-galactosyl and small amounts of L- fucosyl and D-glucuronosyl residues. The size of these side chains varies from one to thirty glycosyl residues (McNeil et al. 1980; McNeil et al. 1982b; Lau et al. 1985; Thomas et al. 1989b; Ishii et al. 1989; An et al. 1994a; An et al. 1994b; Lerouge et al. 1993).

Rhamnogalacturonan-II (RGII) is another pectic polysaccharide that was characterized from sycamore cultured cell walls in 1976 by Alan Darvill and Mike McNeil in Peter's laboratory (Darvill et al. 1978). RGII is highly conserved and is the most complex, branched plant cell wall polysaccharide (Melton et al. 1986; Stevenson et al. 1988b; Thomas et al. 1989a; Puvanesarajah et al. 1991; Whitcombe et al. 1995; Glushka et al. 2003). It can be found as a monomer or a dimer with borate cross links (O'Neill et al. 1996; Ishii et al. 1999). It is composed of approximately 25 glycosyl residues formed by 12 different monosaccharides, including the unusual branched-chain sugar, aceric acid (Spellman et al. 1983a; Spellman et al. 1983b; Vidal et al. 2000) and two keto sugars, 3-deoxy-D-manno-2-octulosonic acid (KDO) (York et al. 1985) and 3-deoxy-D-lyxo-2-heptulogaric acid (DHA) (Stevenson et al. 1988a). Due to its unique structural complexity RGII is highly resistant to degradation by most microbes.

The analysis of plant cell wall polysaccharides requires purification and characterization of enzymes that degrade plant cell walls. The enzymes used in Peter's early studies were purified from fungal and microbial plant pathogens by growing them on cell wall material isolated from plants. Examples of the enzymes that were isolated, purified and characterized in Peter's laboratory include a-L-arabinofuranosidase (Keegstra et al. 1972; Jones et al. 1972), *endo*polygalacturonase (English et al. 1972; Caprari et al. 1994), b-xylosidase (O'Neill et al. 1989), and xylanase (Wu et al., 1995).

Oligosaccharins

Peter's laboratory was the first to discover that oligosaccharides can have a regulatory role in plant defense, plant development and morphogenesis. These oligosaccharides are called oligosaccharins (Albersheim and Darvill 1985). The research into the role of oligosaccharins in plant defense began in Peter's lab at the University of Colorado and continued at the Complex Carbohydrate Research Center (CCRC), University of Georgia. At the time when Peter's group began research on host-pathogen interactions it was already known that certain molecules, called elicitors, caused plant cells to activate some of their defense mechanisms when applied on plant tissues. One of the plant defense mechanisms studied was the release of plant phytoalexins, the antibiotics made by plants at the site where the elicitor was applied. At this time, Dr. Noel Keen

continued on next page

at the University of California, Riverside, was using a soybean cotyledon assay developed by Dr. Jack Paxton. When elicitors were applied onto eight-day-old soybean cotyledons they started production of glyceollin, a phytoalexin, which was detected spectrophotometrically at 286 nm. Peter's graduate student Art Ayers went to Keen's laboratory to learn this soybean cotyledon assay. Art Ayers, Barbara Valent and Jürgen Ebel, a visiting scientist from the University of Freiberg, Germany, were given a task of looking for *Phytophthora megasperma* elicitors using the soybean assay. They found elicitor activity in the culture medium and a hot water extract of *P. megasperma* walls (Ayers et al. 1976a; Ayers et al. 1976b; Ayers et al. 1976c; Ebel et al. 1976). It was a neutral molecule of heterogeneous size with average molecular weight of 1000 Da. However, they found that the highest elicitor activity was released by partial acid hydrolysis of the *P. megasperma* hot water mycelial extract. The smallest active fragment was identified as a hepta-b-glucan. It was shown to be rich in terminal, 6- and 3,6-linked glucosyl residues, indicating that it most likely was a 6-linked pentasaccharide with terminal glucosyl attached to the C3 of two of the 6-linked glucosyl residues. It took eight years to prove that this hypothesis was, indeed, correct. The acid hydrolysis of the *P. megasperma* hot water mycelial extract released 300 different heptaglucosides, but only one had the maximal elicitor activity.

Peter's graduate student Janice Sharp was able to purify the elicitor active fragment by reverse phase column chromatography. She also purified and separated seven inactive heptaglucosides, showing how closely related they are chemically to the active heptaglucoside (Sharp et al. 1984a; Sharp et al. 1984b). The one active and seven inactive heptaglucosides were all neutral molecules with similar structures and properties that made it difficult to separate them. A collaboration with Dr. Per Garegg from the University of Stockholm, Sweden, resulted in the synthesis of the oligosaccharin active heptaglucoside. It was shown to have the same elicitor activity as the natural product (Sharp et al. 1984c).

Peter's graduate student Michael Hahn showed that oligogalacturonides also act as oligosaccharins and elicit phytoalexin accumulation in soybean cotyledons (Hahn et al. 1981). This active oligosaccharin was shown to be a linear 12 galacturonosyl residues long a-1,4- oligogalacturonide (Nothnagel et al. 1983). This was the first fragment of a plant cell wall polysaccharide shown to have oligosaccharin activity.

Oligogalacturonides have also been found to have many other effects on plants (Tran Thanh Van et al. 1985; Eberhard et al. 1989; Mohnen et al. 1990). One effect is to induce tobacco explants to form clusters of flowers, inflorescences, when grown in medium that would produce no flowers in the absence of oligogalacturonides. Peter's graduate student Victòria Marfà showed that only micro molar amounts of active 12-14 galacturonosyl residues long oligogalacturonide were needed to form about five flowers per explant (Marfà et al. 1991).

Peter's graduate student William York found another plant cell wall oligosaccharide with oligosaccharin activity (York et al. 1984). The *endo*glucanase released fragment of xyloglucan was shown to have nine glycosyl residues. It was able to inhibit auxin-induced growth of pea stems. A related seven residue fragment did not inhibit auxin stimulated growth (Augur et al. 1992).

The Complex Carbohydrate Research Center

Peter understood the complexity and difficulty of carbohydrate research. He dreamed of creating a center where researchers from different disciplines would come to work together on the science of carbohydrates. Carbohydrates are complex due to their unique properties and structures and need to be studied using different techniques such as nuclear magnetic resonance spectroscopy, mass spectrometry, genomics, proteomics, etc. Peter envisaged scientists and specialists in these diverse areas coming together to share and exchange ideas, theories and concepts. Dr. Alan Darvill shared the same thoughts and concepts for such a center, which they discussed many times. He had joined Peter's lab as a postdoctoral fellow in 1976 and, over time, they

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PETER ALBERSHEIM ***continued***

had become extremely close friends. In 1984 Peter and Alan started the process to establish a center for carbohydrate research. They and 14 other members of Peter's lab at the University of Colorado moved in 1985 to the University of Georgia in Athens to establish the CCRC. Since then the CCRC has grown to 17 tenure track and many non-tenure track faculty members. The faculty, technicians, graduate and undergraduate students, postdocs, visiting scientists and staff now number over 300 people.

Peter's wife Ivana remembers standing with Peter at the construction site for the current CCRC building. He told her that he always dreamed of having a center for carbohydrate scientific research, but he never thought it would be as big as one that was being built. Today, the CCRC continues to promote carbohydrate research and Peter Albersheim's dream.

Respectfully submitted,
Ivana Gelineo-Albersheim, Alan Darvill, and Karen Howard

References:

Albersheim P. 1963a. Auxin induced inhibition of pectin transeliminase as shown by ozonolysis. *Plant Physiol.* **38:** 426-429.

Albersheim P. 2016. Discovery of oligosaccharins. In: Yin H, Du Y, editors. *Research Progress in Oligosaccharins*. New York (USA): Springer, p. 1-10.

Albersheim P. 1963b. Hormonal control of *myo*inositol incorporation into pectin. *J Biol Chem.* **238:** 1608-1610.

Albersheim P, Bonner J. 1959. Metabolism of hormonal control of pectic substances. *J Biol Chem.* **234:** 3105-3108.

Albersheim P, Darvill AG. 1985. Oligosaccharins: Novel molecules that can regulate growth, development, reproduction, and defense against disease in plants. *Sci Am.* **253:** 58-64.

Albersheim P, Killias U. 1962. Studies relating to the purification and properties of transeliminase. *Arch Biochem Biophys.* **97:** 107-115.

Albersheim P, Neukom H, Deuel H. 1960. Über die bildung von ungesättigten abbauprodukten durch ein pektinabbauendes. *Enzym Helvetica Chim Acta* **43:** 1422-1426.

Albersheim P, Nevins DJ, English PD, Karr A. 1967. A method for analysis of sugars in plant cell wall polysaccharides by gas-liquid chromatography. *Carbohydr Res.* **5:** 340-345.

An J, O'Neill MA, Albersheim P, Darvill AG. 1994a. Isolation and structural characterization of b- D-glucosyluronic acid and 4-*O*-methyl b-D-glucosyluronic acid-containing oligosaccharides from the cell-wall pectic polysaccharide rhamnogalacturonan I. *Carbohydr Res.* **252:** 235- 243.

An J, Zhang L, O'Neill MA, Albersheim P, Darvill AG. 1994b. Isolation and structural characterization of *endo*-rhamnogalacturonase-generated fragments of the backbone of rhamnogalacturonan I. *Carbohydr Res.* **264:** 83-96.

Augur C, Yu L, Sakai K, Ogawa T, Sinaÿ P, Darvill AG, Albersheim P. 1992. Further studies of the ability of xyloglucan oligosaccharides to inhibit auxin-stimulated growth. *Plant Physiol.* **99:** 180-185.

Ayers A, Ebel J, Finelli F, Berger N, Albersheim P. 1976a. Host-Pathogen Interactions IX. Quantitative assays of elicitor activity and characterization of the elicitor present in the extracellular medium of cultures of *Phytophthora megasperma* var. *sojae*. *Plant Physiol.* **57:** 751-759.

Ayers A, Ebel J, Valent B, Albersheim P. 1976b. Host-Pathogen Interactions X. The fractionation and biological activity of an elicitor isolated from the mycelial walls of *Phytophthora megasperma* var. *sojae*. *Plant Physiol.* **57:** 760-765.

Ayers A, Valent B, Ebel J, Albersheim P. 1976c. Host-Pathogen Interactions XI. Composition and structure of wall-released elicitor fractions. *Plant Physiol.* **57:** 766-774.

Bauer WD, Talmadge K, Keegstra K, Albersheim P. 1973. The Structure of Plant Cell Walls II. The hemicellulose of the walls of suspension-cultured sycamore cells. *Plant Physiol.* **51:** 174- 187.

Caprari C, Bergmann C, Migheli Q, Salvi G, Albersheim P, Darvill A, Cervone F, De Lorenzo G. 1994. *Fusarium moniliforme* secretes four endopolygalacturonases derived from a single gene product. *Physiol Mol Plant Pathol.* **43:** 453-462.

Darvill AG, McNeil M, Albersheim P. 1980. General and facile method for distinguishing 4-linked aldopyranosyl residues from 5-linked aldofuranosyl residues. *Carbohydr Res.* **86:** 309-315.

Darvill AG, McNeil M, Albersheim P. 1978. The Structure of Plant Cell Walls VIII. A new pectic polysaccharide. *Plant Physiol.* **62:** 418-422.

Darvill JE, McNeil M, Darvill AG, Albersheim P. 1980. The Structure of Plant Cell Walls XI. Glucuronoarabinoxylan, a second hemicellulose in the primary cell walls of suspension- cultured sycamore cells. *Plant Physiol.* **66:** 1135-1139.

Doares SH, Albersheim P, Darvill AG. 1991. An improved method for the preparation of standards for glycosyl-linkage analysis of complex carbohydrates. *Carbohydr Res.* **210:** 311- 317.

Ebel J, Ayers A, Albersheim P. 1976 Host-Pathogen Interactions XII. The response of suspension-cultured soybean cells to the elicitor isolated from *Phytophthora megasperma* var. *sojae*, a fungal pathogen of soybeans. *Plant Physiol.* **57:** 775-779.

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PETER ALBERSHEIM *continued*

Eberhard S, Doubrava N, Marfà V, Mohnen D, Southwick A, Darvill AG, Albersheim P. 1989. Pectic cell wall fragments regulate tobacco thin-cell-layer explant morphogenesis. *Plant Cell.* **1:** 747-755.

English PD, Maglothin A, Keegstra K, Albersheim P. 1972. A cell wall-degrading endopolygalacturonase secreted by *Collectotrichum lindemuthianum*. *Plant Physiol.* **49:** 293- 297.

Freshour G, Bonin CP, Reiter W-D, Albersheim P, Darvill AG, Hahn M. 2003. Distribution of fucose-containing xyloglucans in cell walls of *mur1* mutant of Arabidopsis. *Plant Physiol.* **131:** 1602-1612.

Glushka JN, Terrell M, York WS, O'Neill MA, Gucwa A, Darvill AG, Albersheim P, Prestegard JH. 2003. Primary structure of the 2-O-methyl-a-L-fucose containing side chain of the pectic polysaccharide, rhamnogalacturonan II. *Carbohydr Res.* **338:** 341-352.

Hahn MG, Darvill AG, Albersheim P. 1981. Host-Pathogen Interactions XIX. The endogenous elicitor, a fragment of plant cell wall polysaccharide that elicits phytoalexin accumulation in soybeans. *Plant Physiol.* **68:** 1161-1169.

Hantus S, Pauly M, Darvill AG, Albersheim P, York WS. 1997. Structural characterization of novel L-galactose-containing oligosaccharide subunits of jojoba seed xyloglucans. *Carbohydr Res.* **304:** 11-20.

Hisamatsu M, Impallomeni G, York WS, Albersheim P, Darvill AG. 1991. A new undecasaccharide subunit of xyloglucans with two a-L-fucosyl residues. *Carbohydr Res.* **211:** 117-129.

Hisamatsu M, York WS, Darvill AG, Albersheim P. 1992. Structure of Plant Cell Walls XXXV. Characterization of seven xyloglucan oligosaccharides containing from seventeen to twenty glycosyl residues. *Carbohydr Res.* **227:** 45-71.

Ishii T, Matsunaga T, Pellerin P, O'Neill MA, Darvill A, Albersheim P. 1999. The plant cell wall polysaccharide rhamnogalacturonan II self-assembles into a covalently cross-linked dimer. *J Biol Chem.* **274:** 13098-13104.

Ishii T, Thomas JR, Darvill AG, Albersheim P. 1989. The Structure of Plant Cell Walls XXVI. The walls of suspension-cultured sycamore cells contain a family of rhamnogalacturonan-I-like pectic polysaccharides. *Plant Physiol.* **89:** 421-428.

Jansen EF, Jang R, Albersheim P, Bonner J. 1960. Pectic metabolism of growing cell walls. *Plant Physiol.* **35:** 87-97.

Jia Z, Qin Q, Darvill AG, York WS. 2003. Structure of the xyloglucan produced by suspension- cultured tomato cells. *Carbohydr Res.* **338:** 1197-1208.

Jones TM, Albersheim P. 1972. A gas chromatographic method for the determination of aldose and uronic acid constituents of plant cell wall polysaccharides. *Plant Physiol.* **49:** 926-936.

Jones TM, Anderson AJ, Albersheim P. 1972. Host-Pathogen Interactions IV. Studies on the polysaccharide-degrading enzymes secreted by *Fusarium oxysporum* f.sp. *lycopersici*. *Physiol Plant Pathol.* **2:** 153-166.

Keegstra K, English PD, Albersheim P. 1972. Four glycosidases secreted by the fungus. *Collectotrichum lindemuthianum*. *Phytochemistry* **11:** 1873-1880.

Keegstra K, Talmadge K, Bauer WD, Albersheim P. 1973. The Structure of Plant Cell Walls III. A model of the walls of suspension-cultured sycamore cells based on the interconnections of the macromolecular components. *Plant Physiol.* **51:** 188-196.

Kiefer LL, York WS, Albersheim P, Darvill AG. 1990. The Structure of Plant Cell Walls XXX. Structural characterization of an arabinose-containing heptadecasaccharide enzymatically isolated from sycamore extracellular xyloglucan. *Carbohydr Res.* **197:** 139-158.

Kiefer L, York W, Darvill AG, Albersheim P. 1989. The Structure of Plant Cell Walls XxVII. Xyloglucan isolated from suspension-cultured sycamore cell walls is *O*-acetylated. *Phytochemistry* **28:** 2105-2107.

Lau JM, McNeil M, Darvill AG, Albersheim P. 1985. The Structure of Plant Cell Walls XV. Structure of the backbone of rhamnogalacturonan I, a pectic polysaccharide in the primary cell walls of plants. *Carbohydr Res.* **137:** 111-125.

Lerouge P, O'Neill MA, Darvill AG, Albersheim P. 1993. Structural characterization of endo- glucanase-generated oligoglycosyl side chains of rhamnogalacturonan I. *Carbohydr Res.* **243:** 359-371.

Marfà V, Gollin DJ, Eberhard S, Mohnen D, Darvill AG, Albersheim P. 1991. Oligogalacturonides are able to induce flowers to form on tobacco explants. *Plant J.* **1:** 217-225.

McNeil M, Albersheim P. 1977. Chemical ionization mass spectrometry of methylated hexitol acetates. *Carbohydr Res.* **56:** 239-248.

McNeil M, Darvill AG, Albersheim P. 1980. The Structure of Plant Cell Walls X. Rhamnogalacturonan I, a structurally complex pectic polysaccharide in the walls of suspension-cultured sycamore cells. *Plant Physiol.* **66:** 1128-1134.

McNeil M, Darvill AG, Albersheim P. 1982b. The Structure of Plant Cell Walls XII. Identification of seven differently-linked glycosyl residues attached to O-4 of the 2,4-linked L-rhamnosyl residues of rhamnogalacturonan I. *Plant Physiol.* **70:** 1586-1591.

McNeil M, Darvill AG, Åman P, Franzén L-E, Albersheim P. 1982a. Structural analysis of complex carbohydrates using high performance liquid chromatography, gas chromatography and mass spectrometry. *Methods Enzymol.* **83:** 3-45.

Melton LD, McNeil M, Darvill AG, Albersheim P, Dell A. 1986. The Structure of Plant Cell Walls XVII. Structural characteri-

continued on next page

PETER ALBERSHEIM *continued*

zation of oligosaccharides isolated from the pectic polysaccharide rhamnogalacturonan II. *Carbohydr Res.* **146:** 279-305.

Mohnen D, Eberhard S, Marfà V, Doubrava N, Toubart P, Gollin D, Gruber T, Nuri W, Albersheim P, Darvill AG. 1990. The control of root, vegetative shoot and flower morphogenesis in tobacco thin cell-layer explants (TCLs). *Development* **108:** 191-201.

Moore PJ, Darvill AG, Albersheim P, Staehelin A. 1986. Immunogold localization of xyloglucan and rhamnogalacturonan I in the cell walls of suspension-cultured sycamore cells. *Plant Physiol.* **82:** 787-794.

Nothnagel EA, McNeil M, Albersheim P, Dell A. 1983. Host-Pathogen Interactions XXII. A galacturonic acid oligosaccharide from plant cell walls elicits phytoalexins. *Plant Physiol.* **71:** 916-926.

O'Neill MA, Warrenfeltz D, Kates K, Pellerin P, Doco T, Darvill AG, Albersheim P. 1996. Structure of Plant Cell Walls XLIII. Rhamnogalacturonan-II, a pectic polysaccharide in the walls of growing plant cells, forms a dimer that is covalently cross-linked by borate diester. *In vitro* conditions for the formation and hydrolysis of the dimer. *J Biol Chem.* **271:** 22923- 22930.

O'Neill RA, Albersheim P, Darvill AG. 1989. The Structure of Plant Cell Walls XXVIII. Purification and characterization of a xyloglucan oligosaccharide-specific xylosidase from pea seedlings. *J Biol Chem.* **264:** 20430-20437.

Pauly M, Albersheim P, Darvill A, York WS. 1999. Molecular domains of the cellulose/xyloglucan network in the cell walls of higher plants. *Plant J.* **20:** 629-639.

Pauly M, Eberhard S, Albersheim P, Darvill A, York WS. 2001a. Effects of the *mur1* mutation on xyloglucans produced by suspension-cultured *Arabidopsis thaliana* cells. *Planta* **214:** 67-74.

Pauly M, Qin Q, Greene H, Albersheim P, Darvill A, York WS. 2001b. Changes in the structure of xyloglucan during cell elongation. *Planta* 212:842-850.

Puvanesarajah V, Darvill AG, Albersheim P. 1991. Structural characterization of two oligosaccharide fragments formed by the selective cleavage of rhamnogalacturonan II: Evidence for the anomeric configuration and attachment sites of apiose and 3-deoxy-2- heptulosaric acid. *Carbohydr Res.* **218:** 211-222.

Sato CS, Byerrum RU, Albershiem P, Bonner J. 1958. Metabolism of methionine and pectin esterification in plant tissue. *J Biol Chem.* **233:** 128-131.

Sharp JK, Albersheim P. 1984. An electron-impact mass-spectrometric fragment-ion that identifies 3-linked D-glucopyranosyl residues in per-*O*-alkylated, linear b-D-glucopyrano- oligosaccharide-alditols. *Carbohydr Res.* **128:** 193-202.

Sharp JK, Albersheim P, Ossowski P, Pilloti Å, Garegg P, Lindberg B. 1984c. Host-Pathogen Interactions XXVIII. Comparison of the structures and elicitor activities of a synthetic and a mycelial-wall-derived hexa-b-D-glucopyranosyl-D-glucitol. *J Biol Chem.* **259:** 11341-11345.

Sharp JK, McNeil M, Albersheim P. 1984a. Host-Pathogen Interactions XXVII. The primary structures of one elicitor-active and seven elicitor-inactive hexa-b-D-glucopyranosyl-D- glucitols isolated from the mycelial walls of *Phytophthora megasperma* f.sp. *glycinea*. *J Biol Chem.* **259:** 11321-11336.

Sharp JK, Valent B, Albersheim P. 1984b. Host-Pathogen Interactions XXVI. Purification and partial characterization of a b-glucan fragment that elicits phytoalexin accumulation in soybean. *J Biol Chem.* **259:** 11312-11320.

Spellman MW, McNeil M, Darvill AG, Albersheim P, Henrick K. 1983a. The Structure of Plant Cell Walls XIII. Isolation and characterization of 3-C-carboxy-5-deoxy-L-xylose, a naturally occurring, branched-chain, acidic monosaccharide. *Carbohydr Res.* **122:** 115-129.

Spellman MW, McNeil M, Darvill AG, Albersheim P, Dell A. 1983b. The Structure of Plant Cell Walls XIV. Characterization of a structurally complex heptasaccharide isolated from the pectic polysaccharide rhamnogalacturonan II. *Carbohydr Res.* **122:** 131-153.

Stevenson TT, Darvill AG, Albersheim P. 1988a. The Structure of Plant Cell walls XXII. 3- Deoxy-D-*lyxo*-2-heptulosaric acid, a component of the plant cell-wall polysaccharide rhamnogalacturonan-II. *Carbohydr Res.* **179:** 269-288.

Stevenson TT, Darvill AG, Albersheim P. 1988b. The Structure of Plant Cell Walls XXIII. Structural features of the plant cell-wall polysaccharide rhamnogalacturonan-II. *Carbohydr Res.* **182:** 207-226.

Stevenson TT, McNeil M, Darvill AG, Albersheim P. 1986. The Structure of Plant Cell Walls XVIII. An analysis of the extracellular polysaccharides of suspension cultured sycamore cells. *Plant Physiol.* **80:** 1012-1019.

Talmadge K, Keegstra K, Bauer WD, Albersheim P. 1973. The Structure of Plant Cell Walls I. The macromolecular components of the walls of suspension-cultured sycamore cells with a detailed analysis of the pectic polysaccharides. *Plant Physiol.* **51:** 158-173.

Thomas JR, Darvill AG, Albersheim P. 1989a. The Structure of Plant Cell Walls XXIV. Isolation and structural characterization of the pectic polysaccharide rhamnogalacturonan-II from walls of suspension-cultured rice cells. *Plant Physiol.* **185:** 261-277.

Thomas JR, Darvill AG, Albersheim P. 1989b. The Structure of Plant Cell Walls XXV. Rhamnogalacturonan-I, a pectic polysaccharide, is a component of monocot cell walls. *Carbohydr Res.* **185:** 279-305.

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PETER ALBERSHEIM *continued*

Tran Thanh Van K, Toubart P, Cousson A, Darvill AG, Gollin DJ, Chelf P, Albersheim P. 1985. Oligosaccharins can manipulate morphogenesis in tobacco explants. *Nature* **314:** 615-617.

Valent BS, Albersheim P. 1974. The Structure of Plant Cell Walls V. On the binding of xyloglucan to cellulose fibers. *Plant Physiol.* **54:** 105-108.

Valent BS, Darvill AG, McNeil M, Robertsen BK, Albersheim P. 1980. A general and sensitive chemical method for sequencing the glycosyl residues of complex carbohydrates. *Carbohydr Res.* **79:** 165-192.

Vidal S, Doco T, Williams P, Pellerin P, York WS, O'Neill MA, Glushka J, Darvill AG, Albersheim, P. 2000. Structural characterization of the pectic polysaccharide rhamnogalacturonan II: Evidence for the backbone location of the aceric acid-containing oligoglycosyl side chain. *Carbohydr Res.* **326:** 277-294.

Waeghe TJ, Darvill AG, McNeil M, Albersheim P. 1983. Determination by methylation analysis of the glycosyl-linkage compositions of microgram quantities of complex carbohydrates. *Carbohydr Res.* **123:** 281-304.

Whitcombe AJ, O'Neill MA, Steffan W, Albersheim P, Darvill AG. 1995. Structural characterization of the pectic polysaccharide rhamnogalacturonan-II. *Carbohydr Res.* **271:** 15-29.

Wilder BM, Albersheim P. 1973. The Structure of Plant Cell Walls IV. A structural comparison of the wall hemicellulose of cell suspension cultures of sycamore (*Acer pseudoplatanus*) and red kidney bean (*Phaseolus vulgaris*). *Plant Physiol.* **51:** 889-893.

Wu S-C, Kauffmann S, Darvill AG, Albersheim P. 1995. Purification, cloning and characterization of two xylanases from *Megnaporthe grisea*, the rice blast fungus. *Mol Plant- Microbe Interact.* **8:** 506-514.

York WS, Darvill AG, McNeil M, Albersheim P. 1985. The Structure of Plant Cell Walls XVI. 3- Deoxy-D-*manno*-2-octulosonic acid (KDO) is a component of the primary cell wall pectic polysaccharide rhamnogalacturonan II. *Carbohydr Res.* **138:** 109-126.

York WS, Darvill AG, Albersheim P. 1984. Inhibition of 2,4-dichlorophenoxyacetic acid- stimulated elongation of pea-stem segments by a xyloglucan fragment. *Plant Physiol.* **75:** 295-297.

York WS, Harvey LK, Guillen R, Albersheim P, Darvill AG. 1993. Structural analysis of tamarind seed xyloglucan oligosaccharides using b-galactosidase digestion and spectroscopic methods. *Carbohydr Res.* **248:** 285-301.

York WS, Impallomeni G, Hisamatsu M, Albersheim P, Darvill AG. 1995. Eleven newly characterized xyloglucan oligoglycosyl alditols: The specific effects of sidechain structure and location on ^{1}H NMR chemical shifts. *Carbohydr Res.* **267:** 79-104.

York WS, Kumar Kolli VS, Orlando R, Albersheim P, Darvill AG. 1996. The Structure of Plant Cell Walls XLII. The structures of arabinoxyloglucans produced by solanaceous plants. *Carbohydr Res.* **285:** 99-128.

York WS, Oates JE, van Halbeek H, Darvill AG, Albersheim P, Tiller PR, Dell A. 1988. The Structure of Plant Cell Walls XXI. Location of the *O*-acetyl substituents on a nonasaccharide repeating unit of sycamore extracellular xyloglucan. *Carbohydr. Res.* **173:** 113-132.

York WS, van Halbeek H, Darvill AG, Albersheim P. 1990. The structure of plant cell walls XXIX. Structural analysis of xyloglucan oligosaccharides by 1H-NMR spectroscopy and fast atom bombardment mass spectrometry. *Carbohydr Res.* **200:** 9-31.