

Peter Albersheim

March 30, 1934 – July 23, 2017



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.

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 β -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 β -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 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 $-4)-\alpha\text{-D-GalAp-(1-2)-}\alpha\text{-L-Rhap(1-$. 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-heptulogonic 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 α -L-arabinofuranosidase (Keegstra et al. 1972; Jones et al. 1972), endopolygalacturonase (English et al. 1972; Caprari et al. 1994), β -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 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- β -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 heptagluco-sides, 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 heptagluco-sides, showing how closely related they are chemically to the active heptagluco-side (Sharp et al. 1984a; Sharp et al. 1984b). The one active and seven inactive heptagluco-sides 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 heptagluco-side. 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 α -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 *endoglucanase* 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 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

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