Wilhelm Friedrich Phillip Pfeffer (1845-1920) [1]

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Wilhelm Friedrich Phillip Pfeffer studied plants in Germany during the late nineteenth and early twentieth centuries. He started his career as an apothecary, but Pfeffer also studied plant physiology, including how plants move and react to changes in light, temperature, and osmotic pressure. He created the *Pfeffer Zelle* apparatus, also known as the Pfeffer Cell, to study osmosis in plants. Pfeffer's experiments led to new theories about the structure and development of plants.

Pfeffer was born in Grebenstein, Germany, on 9 March 1845 to Louise Theobald and Wilhelm Pfeffer [4]. His father owned an apothecary shop inherited from Pfeffer's grandfather and planned for his son to be the third generation owner. His father also owned a large herbarium, a place to house dried plant specimens that are mounted and arranged systematically, and often took his son on expeditions to the countryside. By age six, Pfeffer started his own collection of pressed flowers. Pfeffer's uncle, Gottfried Theobald, also introduced him to nature and the natural sciences, and took him on trips into the Alps starting at age twelve. According to his biographer, Gloria Robinson, Pfeffer was fearless when exploring in the Alps and would search for certain specimens of mosses and rare plants in difficult locations. Pfeffer was one of the first people to climb the Matterhorn, a mountain in the Pennine Alps on the border between Switzerland and Italy.

Pfeffer attended grammar school in Grebenstein until age twelve. He then studied at the *gymnasium* near Kassel. At age fifteen, he apprenticed in his father's apothecary shop. Pfeffer prepared plants, herbs, and ground ingredients. He also made chemicals and medicinal preparations, maintained the shop, and used his father's microscope [5] to examine seed specimens, fibers, and starches. After he passed the test to become an apothecary's assistant, Pfeffer entered the University of Göttingen in Göttingen, Germany, to study chemistry and to prepare for a career in pharmacology. In 1865, four semesters after starting Göttingen, Pfeffer submitted his work, "*Über einige Derivate des Glycerins und dessen Überführung in Allylen*" (Some derivatives of glycerin and their conversion into allyls), and received his doctorate in chemistry and botany.

After receiving his degree in 1865, Pfeffer left the University Göttingen to continue his studies in pharmacology in Marburg, Germany. He received an assistantship at an apothecary in Augsburg, Germany, and then in Chur, Switzerland, where his uncle taught in the state's school. In 1869 Pfeffer passed the examination to become a professional apothecary, but instead he pursued an academic career in botany.

Pfeffer moved to Berlin, Germany, where he obtained a place in the private laboratory of Nathanael Pringsheim, a botanist who investigated reproduction in plants. There, Pfeffer studied the germination of *Selaginella*, commonly known as spikemosses. Pfeffer continued this work with another plant physiologist, Julius von Sachs, in Würzburg. Sachs encouraged Pfeffer to research problems in plant physiology, so Pfeffer began to study the effects of light on how plants decompose carbon dioxide and how stimuli affect plant growth.

In 1871 Pfeffer became a *Privatdozent*, an unsalaried university lecturer, at the University of Marburg in Marburg, Germany. There he submitted his habilitation thesis entitled, "*Die Wirkung farbigen Lichtes auf die Zersetzung der Kohlensäure in Pflanzen*" [The effect of colored light on the decomposition of carbon dioxide in plants]. At Marburg he studied protein metabolism in plants, especially how the amino acid asparagine is formed and diffused in plants. Pfeffer also studied irritability in plants, which means how plants react to changes in environmental factors such as light or temperature. That research led to his investigations of osmosis and osmotic pressure.

After Pfeffer started performing tests on osmotic pressure in plant cells at Marburg, he moved to the University of Bonn [6] in Bonn, Germany, in 1873 where he was a professor of pharmacy and botany. Pfeffer improved on the 1867 experiments of Moritz Traube, who was the first person to prepare artificial membranes and demonstrate their capability to discriminate between water molecules and small solute molecules. Pfeffer used Traube's design for semipermeable precipitation membranes to search for the causes of high osmotic pressure in plant cells. Pfeffer stated the concentration of solutes in cellular water generated pressure. The liquid inside of plant cells pushed on the inner walls of cells and caused their volumes to expand. He called this turgor pressure. He also said that the inner surface of cell walls contained a thin layer of heterogeneous material, and that this layer formed a semipermeable barrier that water traveled through in the process of osmosis. He called this layer the plasma membrane.

To model the plant cell, Pfeffer created his *Pfeffer Zelle* or Pfeffer Cell apparatus using porous porcelain pots and a copper

ferrocyanide membrane. The Pfeffer Cell is a device with many pieces including the porcelain pots, the membrane, measuring tubes, and a pear-shaped vessel containing mercury and water that connects to the other pieces. Pfeffer used his apparatus to study osmosis and to take direct measurements of the solutions at different concentrations and temperatures. His results showed that the concentrations of the solutions affected osmotic pressures in a proportionate relationship. For example, if a membrane separates a sucrose solution from pure water, the concentration of the sucrose solution will be proportionate to the pressure needed to stop water from flowing into the sucrose solution—this is called osmotic pressure. Pfeffer also demonstrated that temperature was directly related to osmotic pressure. He published these results in his book *Osmotische Untersuchungen: Studien Zur Zellmechanik* (Osmotic investigations: Studies on cell mechanics) in 1877. This book provided Jacobus van't Hoff, a physical chemist who worked on the theory of solutions, with values for his calculations on osmotic and gas pressures.

In 1877, Pfeffer became a professor of botany at the University of Basel [7] in Basel, Switzerland, but he moved to the University of Tübingen in Tübingen, Germany, in 1878. For the next nine years he studied how chemicals affect plants. He began working on chemotaxis [8], which is the movement of an organism or cell in response to chemical stimulus. Pfeffer found that capillary tubes filled with a malic acid solution drew the male germ cell of ferns and *Selaginella*, the spermatozoid, to the female sex organ, or the archegonium. Pfeffer's tests showed that chemical agents can affect plant sex organs.

Pfeffer published the book *Pflanzenphysiologie: Ein handbuch der lehre vom stoffwechsel und kraftwechsel in der pflanze* (The physiology of plants: A treatise upon the metabolism and sources of energy in plants) in 1881, which not only presented scientific information, but also included Pfeffer's comprehensive theories on plant physiology. According to Gloria Robinson, Pfeffer was convinced that changes in energy underlay the processes of plant life and that these changes could explain the phenomena of life more generally. In *Pflanzenphysiologie*, Pfeffer discussed the fundamental principles of metabolism and sources of energy in plants. He also covered environmental factors that affect plant growth and development such as light, temperature, and osmotic pressure.

In 1884 Pfeffer married Henrika Volk, and they had a son, Otto, in 1885. Pfeffer then moved to the University of Leipzig [9] in Leipzig [10], Germany, in 1887 to be a professor of botany. He also directed the Botanical Institute at the university. After the death of Pringsheim in 1895, Pfeffer became the coeditor with Eduard Strasburger of the *Jahrubücher für wissenschaftliche Botanik* (Yearbooks for Scientific Botany).

Pfeffer belonged to many societies in Germany and abroad. He received honors and degrees from the universities of Halle, Konigsberg, Oslo, and Cambridge. In 1915 his students dedicated a *Festschrift*, which is a book honoring a respected academic, to Pfeffer, and a special issue of *Naturwissenschaften* (The Science of Nature), a peer-reviewed scientific journal, commemorated his scientific contributions.

Although Pfeffer led a productive scientific life, according to his biographer Erwin Bünning, Pfeffer's last years were increasingly unhappy. He was depressed and haunted by World War I [11], where his only son, Otto, was killed less than two months before the armistice. He was also concerned about the political and social changes happening in Germany. He died on 31 January 1920.

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