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REGULAR ARTICLE

Lorenz Hiltner, a pioneer in rhizosphere microbial ecology and soil bacteriology research

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Abstract Lorenz Hiltner is recognized as the first scientist to coin the term "rhizosphere" in 1904. His scientific career and achievements are summarized in this essay. Most of his research he performed in the Bavarian Agriculture–Botanical Institute (later named the "Bavarian Institute of Plant Growth and Plant Protection") in Munich, where he was the director from 1902 to 1923. Beginning with intensive and thorough investigations on the germination and growth of different crop plants (legumes and non-legumes) Hiltner became convinced, that root exudates of different plants support the development of different bacterial communities. His definition of the "rhizosphere" in the year 1904 centered on the idea, that plant nutrition is considerably influenced by the microbial composition of the rhizosphere. Hiltner observed bacterial cells even inside the rhizodermis of healthy roots. In analogy with fungal root symbionts, Hiltner named the bacterial community that is closely associated with roots "bacteriorhiza." In his rhizosphere concept, Hiltner also envisioned, that beneficial bacteria are not only attracted by the root exudates but that there are also "uninvited guests," that adjust to the specific root exudates. Based on his observations he hypothesized that "the resistance of plants towards pathogenesis is dependent on the composition of the rhizosphere microflora." He even had the idea, that the quality of plant products may be dependent on the composition of the root microflora. In addition to his scientific achievements, Hiltner was very dedicated to applied work. Together with F. Nobbe he had the first patent on *Rhizobium* inoculants (Nitragin). He continuously improved formulations and the effectivity of the *Rhizobium* preparations and he also initiated seed dressing with sublimate for plant protection of seedlings. Thus, Hiltner tightly linked breakthroughs in basic research to improved rhizosphere management practices. In addition, he wrote a pioneering monograph on plant protection for everybody's practical use. His emphasis on understanding microbes in the context of their micro-habitat, the rhizosphere, made him a pioneer in microbial ecology. Even now, in the era of genome and postgenome analysis with our better understanding of plant nutrition and soil bacteriology, his ideas and contributions are as fresh as they were more than 100 years ago.

Keywords Lorenz Hiltner · Rhizosphere · Soil microbiology · Bacteria–plant interactions

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Hiltner's youth, studies and scientific career

Lorenz Hiltner was born on November 30, 1862 in Neumarkt, Upper Palatinate (Oberpfalz), Bavaria, as the first son of a master in acetic acid fermentation ("Essigsiedemeister") and gastronome. His father died rather early. The boy became interested in natural sciences and attended the high school in Neumarkt. He received a scholarship from his home town to attend the industrial school in Nürnberg and to study natural sciences with zoology and botany as major subjects at the University of Erlangen/Nürnberg. In 1882, the very talented young student won a scholarship to study for half a year at the renowned Institute of Zoology at the University of Naples, Italy. Accordingly, his very first publication was entitled "On the development of the *Nervus opticus* in mammals"(Hiltner 1885). After these examinations Lorenz Hiltner refocused his interests on plant sciences and the new scientific field of soil microbiology. In 1885, he joined the institute of Prof. Dr. F. Nobbe, an expert on seed quality control at the Plant Physiological Research Station Tharandt ("Pflanzenphysiologische Versuchsstation Tharandt") near Dresden, Saxony. He learned to connect investigations of plant health with aspects of soil bacteriology and plant nutrition. In the years 1886–1987 Hiltner certainly was fascinated by the news that Hellriegel and Wilfarth had unequivocally proved that the fixation of atmospheric dinitrogen was carried out by root nodule bacteria in legumes. Thereafter, Nobbe and Hiltner themselves conducted intensive studies on the symbiotic interaction of legumes with nodule bacteria in Tharandt. These investigations lead to the first development of bacterial cultures as inoculants called "Nitragin"(Nobbe et al. 1891; Nobbe and Hiltner 1893). In this context, the most important discoveries were the host-specificity of these preparations that determined the applicability of particular strains for certain legumes and the improvement of the formulations to improve their shelf-life. He also conducted pioneering studies on the importance of root nodules of *Alnus glutinosa* for its nitrogen nutrition (Hiltner 1894). During this same period Hiltner also intensively studied plant pathology and methods for microcidal treatments of seeds with mercury chloride. These studies became the basis for his PhD – thesis entitled "Some illnesses of horticultural and agronomical plants caused by *Botrytis cinerea* and their treatment," which was submitted at the University of Erlangen in 1892. These antimicrobial seed treatments provided a significant advantage in agricultural practice and were used routinely until the 1980s. During his stay in Tharandt (Saxony), Hiltner also started intensive surveys of the scientific literature and he refereed the contributions on seed control and plant diseases in the most important German scientific literature on botany, bacteriology and agricultural chemistry. After 14 years in Tharandt, where he became the deputy director of the research station, he left the research station in 1899 to lead the bacteriological laboratory of the department of agriculture and forestry at the famous Imperial Health Institute in Berlin–Dahlem. He could now focus entirely on basic research and continue his fundamental studies on the bacterial community of agricultural soils (Hiltner and Strömer 1903), the germination of legumes (Hiltner 1902) and mycorrhizae (Hiltner 1903). Although Lorenz Hiltner enjoyed the research environment and facilities in Berlin very much, after 3 years, he moved to Munich in Bavaria, where he had been offered a position as founding director of a new agriculture–botanical institute.

Hiltner's first years as director of the Royal Bavarian Agriculture–Botanical Institute in Munich

On October 1, 1902, Lorenz Hiltner (Fig. 1) was appointed as founding director of the Royal Agriculture–Botanical Institute ("königliche agrikulturbotanische Anstalt") in Munich, which later changed its name to the Bavarian Institute of Plant Growth and Plant Protection ("Bayerische Landesanstalt für Pflanzenbau und Pflanzenschutz") in 1917. Besides conducting soil microbiological research, the new institute had the task to support the agricultural practice in Bavaria. He established an organization that supplied farmers with practical information (the agricultural newsletter "Landwirtschaftliche Blätter") and offered seminars for agricultural teachers in so called "winter schools." Hiltner's institute provided farmers with quality tests of seeds, antimicrobial seed dressing with mercury chloride preparations to suppress phytopathogenic fungi at the seedling stage and with diverse rhizobial inoculants. For several years, his institute was the only one worldwide to supply

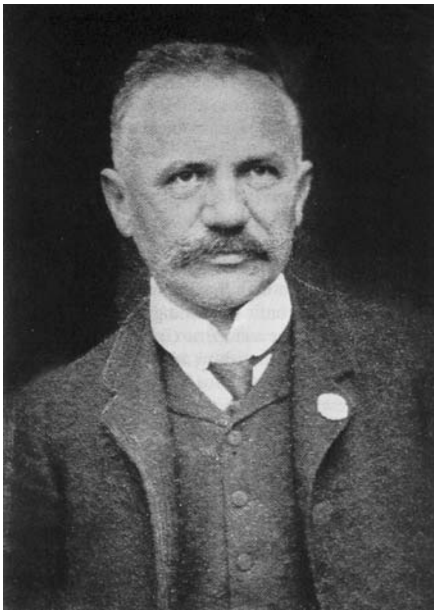

Fig. 1 Dr. Lorenz Hiltner, Founding Director of the Royal Bavarian Agriculture–Botanical Institute in Munich (1902)

farmers with effective rhizobial inoculants. At the world exhibition 1904 in St. Louis, Michigan, USA, Lorenz Hiltner and his Munich Institute won a gold medal for this achievement. In the same year, he received a silver medal at the German horticulture exhibition in Düsseldorf. In 1905, Hiltner was honored to be elected as a foreign member of the Royal Swedish Academy of Agriculture. Scientists from all over the world came to his institute in Munich to learn from his experience. Hiltner organized field experiments with new cultivars and bacterial inoculations in whole Bavaria and gathered a lot of practical experience to improve growth of legumes but also non-legumes. In addition, his institute had to deal with numerous daily problems of agricultural practice and it developed measures to control plant pests like mice and rats. In parallel to these applied tasks of his institute, he continued basic bacteriological research on rhizobia–plant interactions and associations of soil bacteria with Gramineae like wheat and barley.

Definition of the term "rhizosphere" in the year 1904

On April 9, 1904, Lorenz Hiltner gave a lecture at a meeting of the German Agricultural Society (Deutsche Landwirtschaftliche Gesellschaft) in Eisenach, Thuringia, entitled "On new experiences and problems in the field of soil bacteriology with special reference to green manure and fallow"(Über neuere Erfahrungen und Probleme auf dem Gebiete der Bodenbakteriologie unter besonderer Berücksichtigung der Gründüngung und Brache; Fig. 2). This meeting consisted of 14 lectures that provided teachers in agriculture with the latest research developments. In his lecture, Hiltner discussed several aspects of soil bacteriology, which were not directly relevant for the rhizosphere. In the introduction, he talked about his expectations for the application of results derived from basic research, which sound quite familiar even nowadays. "…I would like to state from the very first, that apart from some sporadic exceptions, the main goal of our joint effort, to make the research results applicable in practice, has unfortunately not been reached so far. Some research colleagues even have the opinion that soil bacteriology has to restrict itself to give explanations of facts, which the farmers know already from their experience. […] However, I am convinced that soil bacteriology will finally provide results, which are not only of explanatory nature, but that will directly affect and determine agricultural practice." In the following parts, Hiltner gave examples of a number of cultivable bacteria in soils, that grow on commonly used specific rich media and stated the very modern knowledge that many of the most important bacterial species as well as most of the fungi and algae in soil are not able to grow under these laboratory cultivation conditions on nutrient agar media. Further on, he gave insights into the known bacteria involved in the processes of the nitrogen cycle including denitrification, nitrification and nitrogen fixation, which was the major focus of his lecture. Concerning nitrogen fixing bacteria he referred to the symbiotic bacteria in nodules of legumes, Winogradsky's anaerobic nitrogen fixing *Clostridium pastorianum* and Beijerinck's observation, that free living, oxygen demanding soil bacteria, like *Azotobacter chroococcum*, also display the ability of nitrogen fixation. On page 65, Hiltner expressed very basic ideas about microbial ecology in soils. "… After learning about the different processes involved in nitrogen metabolism, which are catalyzed by organisms freely living in the soil, the most important question arises, how these organisms, probably coexisting in every agricultural soil, interact with each

Fig. 2 Definition of the rhizosphere (translated from Hiltner 1904)

Dr. Hiltner: Über neuere Erfahrungen auf dem Gebiete der Bodenbakteriologie. 59

Über neuere Erfahrungen und Probleme auf dem Gebiete der Bodenbakteriologie unter besonderer Berücksichtigung der Gründüngung und Brache.

Von

Dr. L. Hiltner,

Direktor der Kgl. Agrikultur-botanischen Anstalt München.

Nachdem Herr Professor Behrens bereits vor drei Jahren an dieser Stelle über den damaligen Stand der Forschungen auf dem Gebiete der Bodenbakteriologie in mustergiltiger Weise berichtet hat, erwächst für mich aus dem mir gestellten Thema in erster Reihe die Aufgabe, in Anknüpfung an seine Ausführungen darzulegen, inwieweit sich inzwischen die Erkenntnis der verschiedenen durch Organismen im Boden ausgelösten Vorgänge erweitert und vertieft hat.

Kann ich auch hoffen, Ihnen durch Erfüllung dieser Aufgabe die Überzeugung beizubringen, daß in den letzten Jahren über alle hier in Betracht kommenden Einzelfragen rüstig und auch erfolgreich weiter gearbeitet worden ist, so muß ich andrerseits doch von vornherein erklären, daß, abgesehen von vereinzelten Ausnahmen, das Hauptziel der gemeinsamen Bestrebungen, die Forschungsergebnisse für die Praxis unmittelbar nutzbar zu machen, leider noch nicht erreicht ist, ja daß zurzeit sogar teilweise gerade in den Kreisen der Forscher die Anschauung hervortritt, es müßte sich vielleicht die Bodenbakteriologie für immer mit der Rolle begnügen, lediglich Erklärungen zu liefern für Erscheinungen, die dem schärfer beobachtenden Landwirte an sich schon bekannt sind.

Die überaus große Bedeutung der Bodenorganismen für das Gedeihen unserer Kulturpflanzen wird heutzutage wohl von niemand mehr bestritten; die Wandlungen und Wanderungen des Stickstoffes in der Natur, über die Ihnen gestern Herr Geheimrat Wagner berichtete, sind in ihren Ursachen meist so sicher bekannt, daß wir bereits imstande sind, jederzeit nach Belieben im Laboratorium die betreffenden Vorgänge nachzuahmen, und zwar, soweit sie überhaupt biologischer Natur sind, meist sogar unter Verwendung von Reinkulturen bestimmter Organismen. Auch von solchen Bodenorganismen, deren Bedeutung mehr in ihrem Verhalten gegen kohlenstoffhaltige Verbindungen zu suchen ist, wie den Pektin- und Zellulosevergärern, Humusbildnern und Humuszersetzern, liegen uns manche Arten bereits in Reinkultur vor, und in manchen Fällen können wir angeben, ob irgend ein bestimmter auf Bakterienwirkung beruhender Vorgang auch im Ackerboden unter diesen oder jenen Bedingungen in den Vordergrund treten wird.

other.” Hiltner continued to discuss the relationship between the potential to conduct a certain process (denitrification or nitrogen fixation) and the real activity in a given soil, which provides very different conditions from those used in pure cultures. Depending on the habitat many bacteria can be active in different directions. Furthermore, Hiltner presented the latest results about root nodule bacteria, which he called *Rhizobium beijerinckii* and the progress of inoculation technology, to which he and his research associate Dr. Karl Störmer contributed very much at that time. He discussed the conditions that influence the nitrogen fixing activity of nodules and the effect of soil nitrogen. He also referred to the observation, that oat grew better under mixed cropping conditions with legumes as compared to the monoculture situation, albeit oat is dependent on soil nitrogen. To explain the influence of soil nitrogen on leguminous plants and the enrichment of soil with nitrogen, he argued that this was due to the activity of bacteria in the vicinity of roots that scavenge and store nitrogen. On page 69 he then introduced the term “rhizosphere” as follows: “In soil influenced by roots (Einflusssphäre der Wurzel), or within the “rhizosphere” as I will express myself further on, bacteria take up and immobilize the available nitrogen and thus support and enable the nitrogen fixation of the nodule and the enrichment of the soil with nitrogen. The rhizosphere creates the possibility that these useful activities develop." This is a very broad definition which is still valid nowadays. Hiltner continued to discuss nitrification in the rhizosphere of legumes and in soil and stresses the point of spatial and temporal dynamics in the transformation of nitrogen in the rhizosphere. He presented several examples of positive interactions of plants through rhizosphere interactions. Hiltner stated that during green manuring with legumes not only the nitrogen of the plant, but also the N-content of the rhizosphere is of importance. In this context he stated that nitrogen fixation of legumes and the inoculation with *Rhizobia* is of utmost importance to enrich soils with nitrogen. Hiltner remarked that in his experience the specifically required *Rhizobia* for a given legume crop, e.g. for *Serradella* and *Soja*, are often missing in the soil. He also suggested the application of free-living, N2-fixing and nitrogen scavenging bacteria in non-legumes.

> Key characteristics of the rhizosphere were introduced by Hiltner on pages 75ff:
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> The vision of the rhizosphere of plants implies that detailed studies on the influence of different plant species on organisms living in the root zone must be very promising. It can be assumed with certainty that e.g. the exudations of legume roots attract very different organisms compared to mustard or oat, since each plant species is determined to utilize such organisms, which serve their particular nutritional requirements. The plant is therefore substantially dependent on the composition of the soil microflora in the rhizosphere. The question should be raised, whether part of the different exploration capabilities of plants for certain soil nutrients may be connected to the composition of their rhizosphere microflora. Rhizosphere organisms may partially influence the availability of these nutrients.
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> The extension of the rhizosphere from the root into the soil will certainly depend very much on the soil structure, but in the first place on the plant species. Plants, which exude high amounts of carbonic acid and specific other compounds from their roots, will exert the greatest influence – amongst those the legumes in particular. On the surface of the roots, the bacterial density will reach the highest values. As we could clearly demonstrate, particular bacteria form not only an extensive cover on the root surface, but they even enter the outer cell layers of roots and create a Bacteriorhiza, which may be compared to the Mycorrhiza. In white, very healthy looking and carefully cleaned root pieces of pea with a surface area of 13.8 mm^2 we counted 40.000 bacterial cells; in some cases, the numbers of bacteria on root pieces of the same size reached up to several million.
>
> Since the plant has, on the one hand, the desire to attract beneficial bacteria through its root exudations, it would, on the other hand, be astonishing, if not uninvited guests will also be attracted; they will adapt to the specific root exudates like the beneficial ones. As we could demonstrate, the known cases of soil sickness (tiredness) are indeed caused mainly by the action of those organisms, which enter the roots of plants grown repeatedly on the very same soil. In a three year pot experiment with pea plants grown in the same soil with different levels of fertilization, most severe symptoms of soil sickness were observed in the third generation. The plants looked weak, were easily attacked by pathogens; they turned yellow soon and gave bad yields. Their roots partly appeared rather soft and 3.5 million bacteria of different kind were counted on 1 cm^2 root surface area. Surprisingly, the plants of the fourth generation showed a reduction of these symptoms of weakness. Starting from the fifth generation, the pea plants grew vigorously and the soil sickness was gone. Now, the roots of the pea plants were remarkably brownish on the surface, but white and healthy inside. It could be demonstrated, that a bacteriorhiza had developed, which consisted of adapted beneficial bacteria obviously blocking the invasion by deleterious organisms. An approach seems to be feasible to select for bacteria, which are possibly able to be effective in situations of soil sickness of plants, if this is not caused by faunal parasites or nutrient deficiency. I want to mention in this context, that in soils, in which

> peas develop their beneficial brownish bacteriorhiza, a treatment with the strong disinfectant CS2 (”sulfur carbon“) was clearly not advantageous like in other cases. This treatment completely destroyed the bacterial cover, which functioned as a shield, and it was absolutely deleterious for the growth of the following pea generations. The example, that in the same soil the growth of wheat was improved by a similar CS2-treatment, teaches us the complexity of the interesting relationships between plants and soil organisms. […] According to these observations, the resistance of plants against illnesses is therefore surely dependent on the root microflora. I believe the idea is not too bold, that the quality of the harvest products of our crop plants is substantially influenced by the composition of the rhizosphere microflora. We have already initiated experiments in this direction.

Hiltner continued to discuss the issue of fertilization of agricultural soils and the necessity of the replacement of nutrients to finally obtain good yields according to J. von Liebig's rule. He presented examples that in some agricultural and forest ecosystems, like meadows and mixed forest stands, the yield did not decrease even without fertilization. Consequently Hiltner proposed that the occurrence of nitrogen fixation balances the removal of nitrogen. Hiltner also stresses the point that the nitrogen content of soil humus can be used by many plants possibly through the activity of the bacteriorhiza. Finally, Hiltner discussed the issue of fallow and its importance for soil fertility. He proposed that N-transformations, like nitrification and nitrogen fixation by free-living, N2-fixing bacteria, are very important in this respect. In addition, he stressed the importance of soil humus and humus transformation for soil fertility by providing soil microorganisms with metabolic energy to support their multiple processes. Organic manure seems important in this respect, since it stimulates the formation of humus by its content of complex carbon compounds, which may be even more important than its nitrogen content. At the end of his lecture, Hiltner stated the following (page 78): "I am aware that I have presented more hopes than success stories of the young science of soil bacteriology. Due to the immense complexity of the soil system, our intension to reach an absolute knowledge about the connection of organisms and processes will never be achieved. All too frequently scientists have to state: The truth I seek, but, alas, what truth might be, I have yet to learn."

Hiltner's continued rhizosphere research and his dedication as academic teacher, book author and editor

Lorenz Hiltner was dedicated to his duties as director of the Royal Agriculture–Botanical Institute. He very successfully developed his institute as a place for basic science, but even more as an application oriented organization to serve the needs of the farmers. The staff of his institute increased from four employees (three academics and one technician) in 1902 to about 90 employees (with 14 academic personal) organized in eight departments in 1923.

In his ongoing rhizosphere research in the soil bacteriological department that he led, Hiltner and his coworkers investigated in detail the involvement of the dense bacterial colonization of the root surface and the root epidermis of healthy roots (which he called "Bacteriorhiza") in sustaining plant health. He observed a high incidence of plant sickness when certain crops are planted consecutively over years and explained the phenomenon of "soil sickness" (Bodenmüdigkeit) with the development of pathogens in the rhizosphere. Hiltner reported already about the phenomenon of induced suppressiveness of the bacteriorhiza after several years of consecutive growth of the same crop, in which he observed a recovery which was accompanied with a strong development of the bacteriorhiza on roots of healthy plants. Based on his experiences he hypothesized that "the resistance of plants towards pathogenesis is dependent on the rhizosphere microflora." He even had the idea, that the quality of plant products may be quite substantially dependent on the composition of the root microflora. Hiltner also made continuing field trials to investigate the possibility of plant growth promotion by soil microbes in non-legumes. He had some quite promising results mainly with sugar beet. His basic soil bacteriological and rhizosphere research was cited intensively in the world-wide first comprehensive Handbook on Agricultural Bacteriology

Fig. 3 The laboratories and practical plant protection

("Handbuch der landwirtschaftlichen Bakteriologie") by Felix Löhniss (1910).

Since 1903, Dr. Lorenz Hiltner was appointed as university teacher at the Technical University Munich and in 1908 he became "Honorarprofessor" for agricultural bacteriology. He liked teaching and supervising students very much. Prof. Hiltner was the chief editor of the scientific journal "Praktische Blätter für Pflanzenbau und Pflanzenschutz" (Applied Journal of Plant Growth and Plant Protection). In 1909, Prof. Hiltner published a 433 pages monograph on "Pflanzenschutz nach Monaten geordnet" (Plant Protection over the year's seasons), which presented his great experience and knowledge to a general audience in a systematic and educational manner (Hiltner 1909). Unfortunately, the First World War and the chaotic postwar times disrupted much of his fundamental research. During the war time he conducted intensive studies on alternative food sources for men and livestock to prevent disastrous consequences of the famine in Germany. He published three extensive articles on this theme during these years (e.g. Hiltner 1915). After the war, he managed to start his scientific journal again in 1921 despite the problems with the unstable situation and ongoing revolution and counterrevolution in Munich.

Fig. 4 The Bavarian Institute of Plant Growth and Plant Protection, Munich, Liebigstrasse, 1923 (destroyed during the second World War)

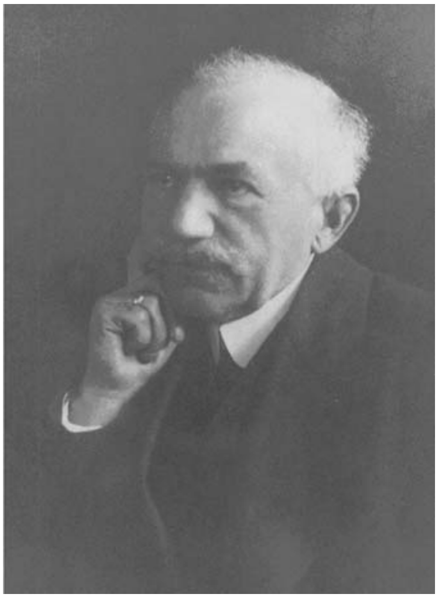

Fig. 5 Professor Dr. Lorenz Hiltner, President of the Bavarian Institute of Plant growth and Plant Protection, München. Picture was taken on his 60th birthday (1922)

In these difficult times, he even managed the construction of a new and much bigger institute building in the city. In summer 1923, his institute was able to move from its original place close to the "Englischer Garten" (English park) in the north of Munich to a new and bigger building in Munich–Lehel in the Justus-von-Liebig-Street (Figs. 3 and 4).

Hiltner's example as great character and scientific leader

Karl Boshart, a coworker of Lorenz Hiltner for many years, described him as an enthusiastic researcher, who was admired by his coworkers because of his quiet and very sovereign attitude as an always very helpful friend and adviser (Boshart 1952). As scientific and academic teacher he gave a lively example of richness of ideas, scientific clarity and dedication to his tasks. Lorenz Hiltner was married since the early times in Tharandt and had three sons; the oldest, Erhard Hiltner, also studied natural sciences and became head of the biological department of his institute in Munich. He continued his father's research and published a second edition of the successful book Plant protection over the seasons. Due to Lorenz Hiltner's research on the biological basis of soil fertility, which places soil organisms and the humic content of soils in central focus, he is recognized today as one of the founders of applied soil microbiology and organic farming. Professor Dr. Lorenz Hiltner (Fig. 5) died unexpectedly of a stroke in his office in the noon hours of June 6, 1923. This left a big gap, since many of his ideas and projects remained unfinished.

Conclusions

Lorenz Hiltner's achievements in basic soil bacteriological and rhizosphere research as well as in practical applications and rhizosphere management had a continuing impact on the understanding of principles of microbe–plant interactions. Later generations added more details to this work, like detailed microscopic views of microbial colonization of the rhizosphere by Rovira in the 1960ies and many more innovative microbiological and agrobiotechnological advances. In the centennial symposium of Hiltner's definition of the "Rhizosphere" in Munich in September 2004, more than 450 scientists gave tribute to his founding work on the rhizosphere and presented studies that continue on many of the ideas first brought to light by Hiltner.

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