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FIFTY YEARS OF RESEARCH IN THE WAKE OF WILHELM PFEFFER

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CONTENTS

1. PREFACE

A few historical remarks, beginning with the nineteenth century, are intended to depict the spiritual atmosphere in which many German biologists of my generation grew up. This atmosphere prevailed because of specific traditions of our schools and universities. It was very different from the situation in the Anglo-Saxon countries.

2. EARLIER EPOCHS: TOO MUCH PHILOSOPHY AND SPECULATION INSTEAD OF EXPERIMENTS

In the nineteenth century, biology in my country was strongly influenced by the so-called *"romantische Naturphilosophie."* These influences can still be detected in the first decades of our century. In France and Great Britain, experimental work in the nineteenth century not only became predominant, but it very nearly replaced pure speculation in astronomy, physics, and biology. In Germany, the influence of certain philosophers remained very strong. This holds for Schelling (1775–1854), Hegel (1770–1831), and Oken (1779–1851). Hegel and Schelling were even directly scoffing at experimental workers. Only a proper world of ideas was considered to lead to any progress in learning about the world. Schelling called Bacon, Newton, and Boyle destroyers of astronomy and physics. Also the famous Goethe must be mentioned here, since his influence in this country was (and still is) very strong. (This holds to a certain extent even with respect to the present days of biology. Certain botanists, especially morphologists still incorporate Goethe's ideas into their publications). Goethe called Newton's optics plain nonsense. He found it more reasonable and rewarding to reflect and to speculate on colors than to look through a glass prism.

This dominating influence of speculation not only prevented experimental work, but also prevented good experimental work from becoming known. The fate of Mendel's discoveries may serve as an example. Mendel communicated the results of his cross-breeding experiments to Carl Wilhelm Nägeli (1817–1891). Nägeli was a famous botanist, but he was indoctrinated by Oken and Hegel. Thus his answer to Mendel was: "your results are only empirical data; nothing in them is rational."

With the beginning of the twentieth century, the situation had somewhat improved. *"Romantische Naturphilosophie"* became weaker, but to mix experimental work with philosophy was still popular. In those years, developmental physiology (or experimental morphology) made rapid progress. Whereas, for example, Wilhelm Roux and Jacques Loeb continued their work without any philosophical prejudice, another of these successful experimental workers, Hans Driesch (1867–1941), just stopped laboratory work and became a philosopher. According to him, the experimental findings with sea urchin eggs clearly proved the correctness of vitalism. One of his arguments: a machine with different structural details in the three dimensions cannot (contrary to the developing sea urchin) reproduce itself when it is disintegrated into its parts. Driesch's influence in philosophy and biology became rather strong. He and his adherents could not foresee that 60 years later Watson and Crick would find precisely such a machine.

The biological literature of those early decades in our country is mixed with many discussions pro and contra vitalism. Also, speculations pro and contra Darwin and pro and contra inheritance of acquired characteristics participated in this mixture of experimental and speculative biology.

In the universities as well as in the schools, philosophy remained the crowning glory of "*Wissenschaft*" (it is very typical that the German term "*Wissenschaft,*" contrary to "science," means nearly everything that is done in universities). Therefore, those who did not accept "*romantische Naturphilosophie*" or vitalism were expected to provide their own philosophy. For example, M. J. Schleiden (1804–1881), one of the founders of the cell theory (i.e. of the concept that the whole body of plants and animals is composed of cells), found it necessary to start his "Grundzüge der wissenschaftlichen Botanik" (1842) with a philosophical introduction of more than 100 pages (especially a strong rejection of "*romantische Naturphilosophie*").

Philosophy forced other people (including well-known biologists) to fight Darwin and, more especially, to be convinced that only environmental factors are responsible for differences between human beings. This led to a defense of Lamarck's hypothesis on the inheritance of acquired characteristics. Paul Kammerer was so much infected by this doctrine that finally he was forced to falsify his own experiments with salamanders. What he as a Lamarckian expected to find in the F_1-generation of dark-adapted salamanders did not occur and had to be done with help of india ink, a manipulation which finally resulted in his suicide (see remarks on "*Weltanschauung,*" section 4).

3. SCHOOLS AND TEACHERS

But there were also factors in this environment with positive effects. The schools in my birthplace (Hamburg) were not an American or German Tennessee; our teachers were allowed to teach Darwin's theories. Darwinism had become rather popular as a result of the activities of the zoologist Ernst Haeckel (who, as a typical German, of course combined his activity with his own philosophy, called monism). We learned also about Gregor Mendel, about the more recent development of genetics, about T. H. Morgan's work with *Drosophila,* etc. (School education before admission to a university in this country is for 13 years, i.e. up to the age of 19, and in my case it lasted until 1925).

By that time not only did Darwinism become popular, but also a great general interest in natural sciences had built up. To collect plants and animals and to observe their development was very common among schoolboys. Many teachers stimulated these interests. School teachers were among the best specialists for certain groups of plants and animals. Whenever a university biologist wanted to know the name of his research object, he knew to which teacher he had to send his material.

Quite a number of teachers in elementary and high schools periodically published in renowned journals of botany, zoology, or geology. Of course this was only possible as long as great advances with magnifiers and microscopes were possible.

So much about influences before joining a university.

4. STUDYING IN GERMAN UNIVERSITIES IN THE TWENTIES

a. The Faculty of Philosophy

My own first university (1925, Berlin) was rather attractive for a student of biology. It was connected with famous names. Berlin was the working place of the Nobel Prize winners Otto Warburg, Otto Meyerhof, and Hans Spemann. Here worked one of the rediscoverers of Mendel's work (Carl Correns); the great plant anatomist Gottlieb Haberlandt was already an Emeritus, but still working. Max Hartmann, who was himself working with both plants and animals, delivered lectures on "general biology."

To join the Berlin university as a student of natural sciences meant to join its faculty of philosophy. Most of our universities still had only the four traditional faculties (theology, medicine, jurisprudence, and philosophy). Only a few universities had at that time founded their own faculty of mathematics and natural sciences. Mathematics and natural sciences were regarded as no more than a somewhat undelicate appendix and tolerated with appropriate condescension. Students, of course, had to respect this; one of our obligatory subjects was philosophy, including a philosophy examination connected with the award of the Doctor of Philosophy degree.

It might be mentioned that the famous botanist Hugo von Mohl (see section 16) was the leading activist in sponsoring the first independent Faculty of Natural Sciences and Mathematics in Germany (1863, in Tübingen). The creation of this faculty was many years behind the creation of corresponding foundations in other European countries. This separation from the Faculty of Philosophy led to long-lasting polemic discussions between von Mohl and the philosophers.

After founding the new faculty, von Mohl and his colleagues just rechristened the Doctor of Philosophy (Dr.Phil.) to Doctor of Natural Sciences (Dr.Rer.Nat.). But this had not yet happened in Berlin during my student days. Many of us appreciated this situation, and did more in philosophy than necessary.

According to a long-lasting tradition in my country, every well-educated man was expected to have and to passionately defend his own "*Weltanschauung.*" This word cannot be translated by "conception of the world" or "world outlook." "*Weltanschauung*" means to combine everything from science, religion, politics, social life, etc into one whole concept. This explains why in my country, even though people are not as hot-blooded as many other nationalities, extreme positions in science or politics are often defended with fanatic obstinacy (see also section 2).

b. "The World's Center of Science"

Philosophy was one of the subjects that also led me to spend part of my student's time at Göttingen. (It was rather an exception in Germany by then for a student to visit only one university). Göttingen already had an independent faculty of mathematics and natural sciences. Also, for a biologist it was a favorable place for his studies in chemistry and physics, again a place with an accumulation of Nobel Prize winners in those fields. Moreover, this faculty had their own philosopher: Leonard Nelson. He had received that professorship especially because of the activity of the mathematicians. Nelson offered a reasonable philosophy to scientists (in some ways a revision and further development of Kant's ideas). Famous people were counted among his friends, for example, the Nobel Prize winner Otto Meyerhof. Also the botanist Friedrich Oehlkers (known for his genetic work) was one of his adherents. Discussions with people such as these allowed long-lasting stimulation, and they offered also a good immunization against the Nazism that was then on the rise. A few sentences from the hitherto unpublished manuscript of Max Born's autobiography may characterize the spiritual situation at Göttingen during the first decades of this century, and the mutual stimulation between physics and philosophy:

> we did a foolish thing: We challenged . . . (Nelson) to a public discussion. . . . This dispute really took place in an overcrowded lecture room of the University, and it ended with a complete defeat for us. . . . we were not prepared . . . to defend systematically our empiristic standpoint. . . . I remained on friendly terms with Nelson . . . he was one of the few who had a vision of the coming catastrophe; he . . . was offended by the reactionary tendency of the time. (A German translation of that manuscript is published: Max Born, "Mein Leben," 1975, Nymphenburger Verlagshandlung, München).

Max Born himself was a famous physicist (Nobel Prize 1954) and inspiring all-around scholar. In his institute at Göttingen, he, together with Heisenberg and Jordan, was just founding the new quantum mechanics during my student days. These new physical aspects stimulated discussion in biology and philosophy already in those years (about 1927), resulting also in another public discussion in an overcrowded lecture room of Göttingen's University (see section 14).

James Franck was a physicist with far-reaching interests (including photochemical processes in chlorophyll). Not only did students find Göttingen to be a place with an especially attractive scientific atmosphere, but they felt (between 1925 and 1930) they were in the world's most important center of modern sciences. James Franck, though he emigrated to the USA during Hitler's time and was involved in the development of the atomic bomb, returned to Göttingen after the war. His wish to spend the last years of his life in that place was fulfilled.

Also many nonmathematicians at times visited lectures or seminars by the famous David Hilbert. Even if his mathematics eluded us, there were always certain utterances which provided rules for our future life, such as: "certain people have a horizon with the radius $r = 0$, and this is what they call their standpoint."

Fascinating for biologists at that time in Göttingen was the Nobel Prize winner Adolf Windaus. In Windaus the biologists admired the man who had detected the chemical structure of vitamins, and thus also stimulated biochemical work. Later on (between about 1930 and 1940), when we were confronted with the mysterious factors "Bios I," "Bios II," "Bios III," and "growth hormone B," we realized that the work by Windaus and his students provided the basis for the demystification of these factors, which were found to be necessary for the growth of fungi.

Last but not least, Göttingen had a special chair for colloid chemistry. Here, R. A. Zsigmondy (Nobel Prize 1925) introduced us into this field. The influence of colloid chemistry on hypotheses concerning structure and functions of the protoplasm became very strong, especially between about 1920 and 1940 (see remarks in section 19). But later, especially with the arising ultrastructural research, it became clear that Graham's (1861) distinction between crystalloids and colloids was not sufficient to meet the characteristics of the protoplasm. The protoplasm is "not a colloidal but a micellar system" (Frey-Wyssling).

Alas, the great heydays of this era were no more to be.

c. From Stamens to the Doctoral Thesis

Our universities offered more freedom in teaching and learning than the universities in several other countries. Freedom did not only mean to esteem liberal thinking. The professors were allowed to teach on whatever subject they wanted to teach, either in their own field or in quite another field. Many people tried to keep alive the illusion of scholars well versed in several disciplines. Moreover, the number of students was rather small, and by the second year of studies the professor could offer his student a rather individual program, in case he found this appropriate. In my second university year, my botany professor in Berlin suggested to me that I just have a look at the flowers of *Sparmannia africana.* The stamens of these flowers belong to the category which show rapid movements on being touched. This "having a look" resulted in my doctoral thesis. I became especially fascinated by the similarities between the processes going on in these stamens and those occurring in animal nerves. There are the periods of latency, the "all or none" type of reaction, the absolute and relative refractory period, the action potentials, etc. This brought me to a study of general physiology. It brought me also to the books and other publications of Wilhelm Pfeffer. Here was the man who clearly had postulated that biology should not be the sum of botany and zoology. He had clearly expressed the thought that there is no difference between animals and plants concerning most of the elementary cell functions. He offered the right approach to a modern biology. According to him, every experiment should only serve as a tool to penetrate to the molecular basis of protoplasmatic functions.

We students during those years enjoyed the same freedom as the professors. Nobody checked whether we were going to a lecture. Nobody checked whether we were reading textbooks. Those who intended to receive the PhD degree had to submit their thesis. After acceptance of the thesis by the faculty, we had to pass our oral examination in three or four subjects (e.g. botany, zoology, chemistry, and philosophy), and this was our first university examination. The German universities, according to a more recent statement from America, were the best in the world—for the nineteenth century. There were optimal conditions to bring into being more research workers. But our universities missed adapting themselves to the changed situation in the twentieth century, especially to the greatly increased number of students.

5. WILHELM PFEFFER'S KNOWN AND FORGOTTEN CONTRIBUTIONS TO BIOLOGY

Studies on rapid movements of stamens guided me to Pfeffer. Pfeffer's studies on the same phenomenon guided him (now more than 100 years ago) to his famous researches on osmosis. He tried to expand stamens which were contracted because of stimulation, by applying counterweights. Thus he hoped to learn about the strength of the osmotic forces which normally are responsible for the re-expansion of the stamens. Result: this re-expansion could not be explained on the basis of osmotic forces as they were known by that time. Thus Pfeffer started to construct his osmometers. His results provided the basis for Van 't Hoff's theory of solutions, distinguished by the first Nobel Prize in chemistry. Comparing Driesch and Pfeffer was a valuable exercise for a young biologist. Both these men were facing phenomena not explainable by known physical facts. Driesch's conclusion: vitalism. Pfeffer's conclusion: research on physical factors.

It is less known or even forgotten that this early work of Pfeffer was already connected with detailed reflections on giant molecules, even including the possibility that the whole plasma membrane (the membrane which is now called plasmalemma) might be a single giant molecule. Actually it was Pfeffer who introduced the concept of a plasma membrane which is distinctly separated from the other protoplasma and which (as he stated) might have a diameter with molecular dimensions.

In present books on membrane biology we may read that, contrary to the classical concepts, membranes no longer should be considered to be filters or sieves. This is true, if we call "classical" the views on membrane permeability as they were offered in textbooks and papers between about 1925 and 1950, in which we read about "ultrafilter theory" on the one hand and "lipoid theory" on the other hand. It has been forgotten that Pfeffer nearly 90 years ago, i.e. long before this so-called classical period, warned passionately against a concept which is now called classical. His view was that plasma membranes are active; they can select like a doorkeeper. Pfeffer even mentioned the possibility of carrier molecules, as they are now called.

People have almost forgotten that 90 years ago Pfeffer with his studies on chemotaxis of bacteria, found that bacteria are able to distinguish qualitatively different substances. These studies on "specific sensitivities" of unicellular organisms were continued in Pfeffer's laboratory for several years. The results allowed Pfeffer to state (1893) that the senses of unicellulars are not poorer than those of vertebrates. For most of his listeners this was perhaps more shocking than a related statement by Monod and Jacob: "Anything found to be true of *Escherichia coli* must also be true of elephants" (1961). Pfeffer's conclusions were neglected until around 1960, when Julius Adler (in Madison) resumed studies concerning this problem.

It is often believed that the discovery of adaptive enzymes is one of the laurels of modern microbiology. But actually this discovery was made in Pfeffer's laboratory shortly before 1900 and continued to be a topic of research in that laboratory for several years. Pfeffer stated that three or four units should be sufficient to yield all of the necessary information for an organism's development. He suggested using bacteria for studying evolution.

6. PFEFFER, GOETHE'S MORPHOLOGY, AND THE MODERN "NEW CONCEPTION OF MORPHOLOGY"

The term "morphology" was introduced by Goethe. In addition, Goethe is the father of the concept that all the external parts of the plant shoot are due to the transformation of one organ, i.e. of the ideal leaf. This organ, as well as the shoot and the root, was itself considered an abstraction and something like the realization of an idea. This concept in its original strict version used to be called *"idealistische Morphologie"* in German books. It is another child of *"romantische Naturphiloso-phie."* Several German authors (for example, the great morphologist Wilhelm Troll) are continuing to support this orthodox version (though experimental morphologists presented facts which hardly fit this doctrine; consider, for instance, the experiments by C. W. Wardlaw). Others silently allowed *"idealistische Morphologie"* to be buried.

Nevertheless, parts of Goethe's concept are still alive, for example, in the convention of absolutely distinguishing between analogous and homologous organs. To many biologists it was almost a shock when Sattler recently risked an open declaration of death for this old morphology (R. Sattler, 1973. A new conception of the shoot of higher plants. *J. Theor. Biol.* 47: 367–82). He suggested a new model, no longer assuming strict limits between shoots, leaves etc, but allowing transitions between the several organs. Sattler could not have known that Pfeffer made the same statement exactly 100 years earlier. During his *"Habilitation"* in 1871 (examination to become admitted as a lecturer), the first of the theses which he had to present and to defend was "root, shoot, leaf, and hair are not mutually exclusive; transitional forms connect them with each other." (The theses are not published. They are preserved in Hessisches Staatsarchiv, Wiesbaden, Germany.)

The reflections by Sattler are conclusions from the modern development of experimental morphology. For botanists of my generation it was rather fascinating to see old morphological problems becoming more and more integrated into physiology. Karl von Goebel (1855–1932), himself one of the first experimental morphologists, still teased morphologists by writing that "morphology is what cannot yet be explained by physiology."

This early statement by Pfeffer on morphology is part of Pfeffer's general concept concerning basic principles of modern physiology. He warned not to treat organisms as isolated entities in nature. Both with respect to metabolism and to energetics they are nothing else than a whirl in the great universe. Heeding the warnings would also have prevented many later speculations on the organism's ability to work contrary to the principles of the second law of thermodynamics. Pfeffer clearly expressed that the subdivision of natural sciences into physics, chemistry, and biology is nothing but an arbitrary act introduced for pragmatic reasons.

7. CIRCADIAN RHYTHMS AND PFEFFER'S MISTAKE IN PUBLISHING IN A "WRONG" JOURNAL

Friedrich Dessauer, radiologist in Frankfurt at the "Institut für Physikalische Grundlagen der Medizin," was interested in the effects of the ionic content of the air on humans. In the 1920s the interest in possible effects of atmospheric electricity and cosmic rays on organisms was increasing. In 1928, Dessauer engaged, with postdoctoral fellowships, two botanists in order to start experiments with plants. One was Kurt Stern, the other was I. Searching for possible phenomena in plants which might be influenced by atmospheric factors such as those mentioned, we started to study diurnal leaf movements. There were several facts indicating the synchronizing effects of some unknown factor on these movements. The maximum night position of bean leaves in continuous darkness was reported to occur mostly about 3 hr after midnight. Our first experiments confirmed this result. But later on we decided to look for better conditions than those offered to us in the institute. We experimented with temperature control in a cellar of Kurt Stern's private house. Our experiments in that cellar differed from our earlier experiments and from those of earlier researchers in the fact that we no longer started them in the morning but rather in the evening. The result: most of the maximal night positions no longer occurred 3 hr after midnight but about 8 hr later. It was a short step to discover that the weak red light, used for the necessary manipulations to start an experiment, was the synchronizer. (In those years textbooks maintained that red light had no effect at all on any type of plant movements.) It was also a short step to find a free-running period deviating from the exact 24 hr cycle. But it was a long way before others discovered phytochrome, the receptor for that red light.

Several years later I found in a booklist offering second-hand books a paper published by Pfeffer in 1915. In this paper Pfeffer clearly disproved his earlier stand against the assumption of an endogenous diurnal periodicity. It is a long paper with many experiments showing entrainment of the rhythms by light-dark cycles deviating from the 24 hr period, showing phenomena such as "frequency demultiplication," showing free-running periods deviating from the 24 hr period, etc. Pfeffer's only mistake was to publish it in the *Abhandlungen der math.-phys.Klasse der Königl.Sächs.Akad.d. Wissenschaften.* It was not customary to look into such a journal for that kind of material. Pfeffer's experimental conditions were definitely better than those used by us and by other botanists after Pfeffer. He had not only constructed a room with constant temperature himself, but also (about 70 years ago!) rooms with automatic switching to provide various light and dark periods, including simulation of dawn and dusk conditions.

I still had many scientific communications with Kurt Stern after this time (mainly on energetics and electrophysiology). The last letter I received from him was written in 1934 from France. He then moved to the USA, but could not find conditions which allowed him to survive: He became one of the many victims of Hitlerism.

8. CIRCADIAN RHYTHMS AND PHILOSOPHY

It is easy to understand why anyone proclaiming the existence of an endogenous diurnal periodicity was regarded as a mystic. The philosophical positivism being rather generally accepted as a counterbalance against philosophies such as those mentioned in section 2 believed experiences to be the only source of knowledge concerning the outer world. Jacques Loeb's theory of tropism is a typical example of influences of this concept in physiology. He tried to explain fully the behavior of animals and humans as resulting from a network of tropisms induced by external factors. (By the way, Loeb started with this idea when learning about plant tropisms in the laboratory of Julius Sachs). When, according to the theory of the behaviorists, even the mind of humans at birth is a "clean slate," how could a plant "know" something about the temporal structure of the outer world before "birth"? Konrad Lorenz strongly rejected this behaviorism, and recently Gunther S. Stent stated "The a priori concepts of time ... (etc) happen to suit the world because the hereditary determinants of our highest mental functions were selected for their evolutionary fitness . . . which require no learning by experience" (G. S. Stent, 1975. Limits to the scientific understanding of man. *Science* 187:1052–57). This assertion holds much relevance for the behavior of plants.

It might strike one as a frivolous exercise to compare the inherited "knowledge" of humans with the inherited "knowledge" of plants about 24 hr days. But the evidence to link these two facts is not missing. Around 1940 I became not only familiar with the works of Konrad Lorenz (Nobel Prize 1973), but also with those of the ingenious zoologist Erich von Holst. Von Holst had been demonstrating the existence of inherent rhythms in the central nervous activity of fishes, rhythms underlying rather complex patterns of locomotory behavior. Niko Tinbergen (Nobel Prize 1973), after writing about Lorenz's work, called von Holst "another individual heretic" (N. Tinbergen, 1969. Ethology. In *Scientific Thought 1900–1960,* ed. R. Harré, Oxford).

Thus the results of research work in plant physiology, in zoology, and in psychology help in rejecting the "clean-slate-at-birth hypothesis" of philosophers, pedagogues, etc.

9. DARWIN, HABERLANDT, THE MOON, AND THE CIVIL TWILIGHT

Circadian leaf movements belong to the small group of complicated physiological processes for which until recently no adaptive value was obvious. Linné found these movements suitable for allowing humans to find the time of day (see section 12). Other researcher workers found the movements suitable for detecting endogenous diurnal periodicity. But another aspect of these movements was neglected in spite of Darwin's statement "that these movements are in some manner of high importance to the plants which exhibit them, few will dispute who have observed how complex they sometimes are." They are indeed very often by far more complex than the simple up and downward movements as in the case of beans or soybeans. And why is it "a very common rule that when leaflets come into close contact with one another, they do so by their upper surfaces, which are thus best protected . . . it is obviously for the protection of the upper surfaces that the leaflets . . . rotate in so wonderful a manner . . ." (Darwin)? But, of course, for recording leaf movements, the physiologist prefers the simple cases.

At the turn of the century Haberlandt raised another question which remained unsolved for a long time. It is a problem which is connected with Darwin's question. Haberlandt, in detailed studies of the anatomical and optical properties of the leaf epidermis, concluded that the upper epidermis functions as a sense organ for light. He published a whole book on this special question in 1905, but experiments to check whether those structures are important for phototropic movements did not bring the expected results. Covering the epidermis with oil and thereby avoiding the lens effect did not reduce the phototropic responsiveness (Kniep, 1907). Nevertheless, modifying Darwin's formulation, we may state "that these structures (lenses and ocelli in the epidermis) are in some manner of high importance to the plants, few will dispute who have observed how complex they sometimes are." They are far more complicated than in the leaves which for good reasons we select when teaching plant anatomy.

Combining the observations of Darwin and Haberlandt with well-known facts about photoperiodic threshold light intensities during the periods of civil twilight with knowledge about the intensity of moonlight and with new experiments helped to form, I hope, an answer to those open questions.

The leaves indeed proved to be masters in cybernetics. For too long a time they were believed to be mainly organs for photosynthesis and transpiration. The stomata were believed to be the only interesting cells in the epidermis. Now it is clear that the chlorophyll-free cells of the epidermis are the main receptors for photoperiodically active light. It is also clear that leaf movements can help to increase accuracy in measuring the length of the day from morning until evening civil twilight, as well as in preventing moonlight from being misleadingly interpreted as "long-day."

General conclusion: It may also be advantageous sometimes to look into old literature and not to restrict ourselves always to the simplest systems.

10. WORKING IN A GERMAN BOTANY DEPARTMENT IN THE THIRTIES

a. Jena around 1930

In the years around 1930 it was very difficult to find a position. Thus I was extremely happy to be offered an assistantship in Jena in 1930. Jena had one of the larger botanical institutes of Germany. In most of our universities these departments were smaller, but the conditions which I found in Jena were rather representative. The botany tradition in Jena goes back to Goethe. The house where he used to stay in Jena was still present in the botanical garden during my time there. Goethe had given the first advice for that garden. It is not amazing that "*romantische Naturphilosophie*" also had some influence in Jena. One of the early professors responsible for the garden (Schelver, from 1802–1806) stated that Cammerarius' discovery of sexuality in plants (in Tübingen in 1694) should not be accepted. He deduced from philosophy that this is just impossible. Philosophy, of course, was believed to be more reliable than experiments. According to Schelver the spreading of pollen grains was nothing but the plant's efforts to get rid of bothersome substances. But later on, famous pioneers in several fields of botany worked in Jena: Schleiden, Pringsheim, Strasburger.

Even at my time, there was only one full professor ("*ordentlicher Professor*"), at that time the geneticist Otto Renner. In those early 1930s he clearly demonstrated with his *Oenotheras* the presence of genetic information in plastids. Furthermore, there was an associate professor ("*ausserordentlicher Professor*"), but he was especially responsible for teaching the pharmacy students. In addition, there were two assistants. The other assistant besides myself was Leo Brauner. There was a housekeeper who, together with his wife, had to care for the cleaning of the building, for making toilet paper from old newspapers, etc. There were no technicians, no secretary.

The tasks of an "assistant" were: supervising the students' laboratory work for at least 4 hr every day (including Saturday); during the months between the terms to prepare material for lectures and laboratory work for the next term, again at least 4 hr per day. The assistant was also responsible for any work which nowadays is done by an administrator, a technician, or a secretary, such as typewriting, making slides, caring for all business affairs, supervising the small budget, etc. During the summer term he had to prepare for the great general botany lecture of the professor. This meant starting not later than 7 A.M. by bringing all the material to the lecture hall: higher and lower plants, all in the right developmental stage, fresh microscopic preparations, and many experimental demonstrations for the various fields of plant physiology. By that time most of our botany professors had learned these demonstrations from Pfeffer, and Pfeffer had been the inventory of many of the methods used. Right after the lecture, which was from 8–9 A.M., we had to start preparing the lecture for the following day. Sometimes this required the whole day and also the evening hours. The salary was 160 marks (about 65 US dollars) per month. This was much less than the salary for a teacher in an elementary school. But we found this to be fair. After all we had the chance to receive—in case of further successful research work—the title of (an unpaid) professor at the age of about 35 years, and even the chance for a paid professorship between the ages 40 and 45. Many waited in vain for the realization of this dream and remained assistants for their entire lifetime. In those years, according to public opinion in Germany, being "Herr Professor" meant more than to drive a Rolls Royce or a Mercedes.

There were no grants for joining congresses, though we were expected to participate at least in the annual meetings of the German Botanical Society. After all, these meetings were the marketplaces where we could offer ourselves.

Of course, if an assistant had become lecturer ("Dozent," after "Habilitation") in the minimum two years after receiving his doctorate degree), he still had to go on with his assistant work, and his own lecture could not be presented within his business hours. Brauner had his first lecture from 12–1 P.M.; from 8–12 he had to supervise students' laboratory work. Once he found it necessary to look into his manuscript a few minutes before 12. The professor happened to come by, looked at his watch, and reprimanded "it is not yet 12."

This seemed to us to be rather normal and almost self-evident. Equally self-evident was buying the paper, pencils, ink, etc. for our publications with our private money. The professor also observed these rules. He also wrote everything himself (notes only on the reverse of calendar sheets), and he too worked from 8 in the morning until late in the evening, including all of Saturday and half of Sunday. No professor or assistant ever contemplated becoming a criminal by misusing the official electricity or gas for making a cup of coffee. We knew that professors in other universities had the same style of living and working. Pfeffer started lecturing sometimes at 6 A.M. and he too worked until late at night. Julius Sachs, known as the founder of modern plant physiology, asked a student who was leaving the laboratory before 8 P.M. whether it was a holiday. He himself started laboratory work during the summer season sometimes at 4 A.M.

b. Jena during the "Third Reich"

How much good reason we had to trust and to admire our professor (Otto Renner) became clear in 1933, after Hitler's victory. The majority of the students were supporting the Nazis. The great majority of the professors were by tradition liberal, but unfortunately with no sense of political involvement. Most of them started to make compromises. But in May of 1933, Renner risked a very strong public attack against the Nazis. In the introduction to a seminar he described the great role of Jewish scientists in Germany, and he defended Leo Brauner, a Jew who at that time was already forbidden to enter the institute. It was mainly the students' activity which forced Leo Brauner to leave Jena so early and to emigrate via England to Turkey. I was believed to be too red, and this forced me to leave Jena two years later. Long-lasting contacts with both Renner and Brauner survived those bad years and even the war.

In the fall of 1944, a few months before armistice, Otto Renner reported in a scientific society on the history of the Jena Botanical Institute (published 1947). The situation by that time may be illustrated by mentioning his additions to the manuscript of his report:

> Addition to manuscript: the institute was still unhurt when reading of the paper was announced to the Society. While reading the paper, one part of the building was fully destroyed, the other part severely damaged, most of the greenhouses destroyed. Addition in first proof: now the Goethe house is damaged, the rest of the greenhouses destroyed by bombs, the garden ransacked. Addition to second proof, May 9, 1945: Gunfire from artillery resulted in further severe damages.

c. The Carl Zeiss Firm and Botany

The main reason for bombing Jena was of course the presence of the famous firm of Carl Zeiss. It was no longer a secret that they produced more than microscopes. Before the war, the presence of that firm offered great advantages. The university would not have been able to maintain its great activity without the continuous help from the Zeiss Foundation. For example, I had only to write a letter in order to get a photometer gratis. When Renner was offered a chair at another university the Zeiss Foundation, in order to retain him, took care of building a house for his private use and also helped to provide him with an experimental field for his genetic experiments with *Oenothera*. This again was helpful for my studies on circadian rhythms. I was allowed to use part of that experimental field for my cross-breeding experiments with *Phaseolus* strains having different lengths of circadian periods. Doing this in close contact with a geneticist was certainly helpful.

The Zeiss firm had good reason to be grateful toward the University of Jena, and especially to the botanists. It was Schleiden whose intercession on behalf of the then unknown mechanician Carl Zeiss enabled him to obtain a license for establishing his workshop in Jena in 1846. Schleiden also gave the decisive impetus for the specialization of the workshop in the production of microscopes. The cooperation between Zeiss and the University of Jena resulted also in making Jena something like a germ-cell of fine-structure research in biology. In 1899 Hermann Ambronn got the chair for scientific microscopy which was founded by Ernst Abbe (the decisive man in the Zeiss firm). Ambronn's work in Jena was especially the application of the polarization microscope. The conclusions concerning the fine structure of different organic and inorganic materials allowed an early combination of biological research with the budding field of colloid chemistry and the subsequent beginning of macromolecular chemistry. Ambronn clearly proved the existence of those "micells" which Carl Nägeli had postulated in 1884. The successful continuation of that work by Ambronn's student, Frey-Wyssling, is also well known to younger biologists.

11. THE *AVENA* COLEOPTILE AND CONSEQUENCES OF NEGLECTING PHYSICS

For a younger biologist it was not considered advisable to restrict his research to the so-called mysterious endogenous diurnal periodicity. Thus I decided to join the better-appreciated research on phototropism. This brought me especially to studies on the role of carotinoids in phototropism of *Pilobolus, Phycomyces,* and *Avena.*

Concerning phototropism there were (even in textbooks) long-lasting discussions on whether only the direction of the offered light or gradients of its absorption were responsible for the phototropic effect. With better training of botanists in basic physical laws these discussions would have been prevented. Most of our botanists did not know that only absorbed light can exercise any physiological effect. This defective training explains also why only in the 1930s were the first successful attempts made to draw conclusions from action spectra and to search for the absorbing pigments. At the beginning of the thirties it was well known that only blue and UV light are effective in phototropism. But the usual explanation was based on the higher energy of the quanta in these regions. Great progress was heralded by Johnston's finding a phototropic action spectrum with two peaks in the blue light region (E. S. Johnston, 1934. *Smithsonian Misc. Coll.* 92, No. 11) But it was only a year later that the similarity of this action spectrum to the absorption spectrum of carotinoids was found worthy of mention (E. S. Castle, 1935. *Cold Spring Harbor Symp. Quant. Biol.* 3:224–29). The first hints suggesting carotinoids led to the search for common features in light-absorbing "visual" systems of plants, unicellulars with eye spots, and animals. Searching for this phylogenetic sequence meant again to have learned unconsciously from Pfeffer that all the various "senses" of plants and animals are already programmed in unicellulars. He wrote in 1893: "This elementary species, the protoplasm, contains the whole secret of life, and consequently, every type of response is inherent in it. It is for this reason that even the simplest organism, be it bacterium or myxomycete, is just as sensitive to stimuli as a higher plant."

12. FROM LINNE'S FLOWER CLOCK VIA CIRCADIAN RHYTHMS TO THE BIOLOGICAL CLOCK

Carl von Linné (Linnaeus) "constructed" a "Flower Clock." He collected data on opening and closing times of flowers from various species. He stated that these data might help people walking in the fields without a watch to find the time of day. Physiologists were more interested in finding the underlying processes: thermonasty, photonasty, and circadian rhythmicity. For those who followed Pfeffer's recommendation that plant physiologists should read what animal physiologists have published, it was easy early in the 1930s to find and to evaluate the papers by Kalmus on eclosion rhythms in *Drosophila* and by Beling (in von Frisch' laboratory) on the time sense of bees. It became evident that we were dealing with a more general phenomenon. This stimulated me already at that time to incorporate insects into my research program and to contemplate concerning time-measuring functions of circadian rhythmicity.

But when in 1935 I announced a paper on endogenous diurnal periodicity in animals and plants for the annual meeting of the German Botanical Society, I was asked whether I should not better restrict myself to plants, since this was a meeting of botanists. To combine hypothesizing, making experiments, and discussing was very helpful also in this case. There was, for example, a meeting in Berlin (I think it was in 1942) organized by Georg Melchers and Anton Lang. The discussion resulted in certain predictions. One of the predictions was the possibility of replacing the effect of long days (both for long-day plants and for short-day plants) by applying short days with a light break in the dark period. Many additional experiments with longer lasting dark periods also resulted from these discussions. Due to the wartime conditions, I was able to the see the papers by Naylor and by Rasumov (both published in 1941), reporting this light-break effect, only several years after their publication.

In the earlier years of research on photoperiodism, this phenomenon was too often treated as a specific problem of flower formation. There were even trends to unify these two subjects. Only later on did it become clearer that photoperiodism is a control mechanism which can be incorporated in a great variety of developmental processes of plants and animals. In certain cases each of these various processes can go on without being coupled to that control. I learned this in the tropics.

13. LEARNING IN THE TROPICS

Trees in which the several twigs and branches follow their own developmental rhythm (i.e. are not synchronous with other twigs of the same individual tree) clearly demonstrate temporal relations between the development of leaves and flowers. However, the additional occurrence of flower formation in cauliflorous plants (flowers emerging from the bark of the stems without relation to the developmental cycles of the leaves), and of parasites such as *Rafflesia* and *Balanophora* (having no leaves in their vegetative stage) brings another important piece of information. These facts show that flower formation can be quite independent of leaves.

The insertion of the leaves (being the site of photoperiodic light reception) into the chain of the developmental processes leading to the flower formation is only a secondary adaptation. But without this insertion, the great accuracy of photoperiodic time measurement would not have been possible. A location of photoperiodic light reception in the growing point would not have allowed the cybernetic tricks mentioned in section 9.

These observations on flowering were one of the stimulating effects of my looking around in the tropics. Another example: It is well known to botanists that the idea of the possibility of circannual rhythms originated long ago from studying developmental cycles in the tropics. Those observations led to discussions by Darwin and by several botanists (including Pfeffer). During the last 25 years the earlier conclusions have been confirmed in several laboratories by experiments under controlled conditions. Recently the papers of a symposium on circannual rhythms were published. In spite of its general title it refers only to findings on animals, and none of the great number of earlier reports concerning plants is mentioned. As early as 1893, Pfeffer stated: Animal physiologists should know what plant physiologists are doing and vice versa. And the recent suggestion to print scientific papers only on paper decomposing itself within a few years needs some serious rethinking in this context.

In the famous Botanical Garden of Buitenzorg (Bogor) in Java I also found collections of data concerning developmental cycles of various tropical plants. Here I learned, for example, that the famous *Amorphophallus titanum* with its 2 m long inflorescences requires about 30 months for one developmental cycle (including leaf formation, flowering, rest period). I learned, for instance, that other species of plants require only 6–10 months for one cycle. This was a clear demonstration that circannual rhythmicity in nontropical plants could have evolved by selection from that great variety of periods. A demonstration of a similar kind is not possible concerning the evolution of circadian rhythmicity.

Actually, from the very beginning of this century the studies on developmental cycles of tropical plants were closely connected with the laboratories in that garden. For example, Klebs, the first discoverer of photoperiodism in plants (1913), made great efforts in 1910 and 1913 to find external factors influencing the periodicity of tropical plants, whereas others before him had concluded the participation of internal factors.

The great lake in the Buitenzorg garden provided fine material for work on circadian rhythms: small sections of the petals of tropical *Nymphaea* species continued with their circadian rhythms in growth and in CO_2 output under constant conditions.

14. EINSTEIN: "GOD DOES NOT PLAY DICE." DO ORGANISMS PLAY DICE?

Our old German tradition of making new philosophies as soon as new scientific aspects are uncovered continued long after the times of Driesch and Haeckel. The modern virus research led to long-lasting discussions, even to the writing of whole books, concerning the question of whether a virus is a living entity or not. These discussions were reminiscent of medieval theological disputations.

A stronger philosophical stimulus came from quantum mechanics, especially from Heisenberg's formulation of the uncertainty principle (1927). According to this principle, it is impossible to determine simultaneously the position and the momentum of an electron. Microevents were no longer assumed to be predictable. The classical laws of physics were stated to be valid only as far as we are dealing with large groups of particles. Albert Einstein did not immediately agree with this new development. His reaction was: "God does not play dice." But for others the uncertainty principle was even a key for understanding the secret of life.

Pascual Jordan used Heisenberg's principle for evolving a new concept of biology. According to him, the organisms do not follow the classical laws of physics. He made a reinforcement hypothesis; accordingly, it was not large groups of particles that were at the basis of the biological processes, but rather unpredictable microevents in the sense of the quantum mechanics. Whole books were written concerning this hypothesis. Many old problems on the borderline between biology and philosophy, such as that of the freedom of will, were made to fall in line with this principle of uncertainty. Heisenberg (keeping aloof of these speculations) and P. Jordan had started their work on quantum mechanics around 1925 at Göttingen. A few years later I became involved in discussing Jordan's hypothesis. For a biologist it was (and is) immediately clear that only certain biological phenomena (mutation, new combination of genes) are based on the principle of "playing dice." The secrets of physiological processes cannot be found in the principle of uncertainty. The typical expediency of physiological processes is only possible with strict causality. That means that in spite of the molecular dimensions of biological control mechanisms, the organisms try to avoid microphysical accidents. (They cannot absolutely prevent the occurrence of that sort of accidents, as, for example, in the mistakes in transcription from the DNA).

The birthplace of quantum mechanics, i.e. the University of Göttingen, invited Pascual Jordan and me in 1944 for a public discussion on that question. Jordan's ideas had stirred many people from various fields. This explains why in spite of wartime the auditorium was filled with biologists, physicists, philosophers, theologians, etc. Fortunately, no air raid alarm interrupted the discussion that lasted a long time. The biologists participating in this discussion were helping me, and I was quite happy with the evening. But later on I had to learn the bitter truth that arguments normally do not convince founders of religions and philosophies.

Rejecting the hypothesis that organisms work on Heisenberg's principle of uncertainty is not to reject Niels Bohr's statement that "This revision of the foundations of mechanics... has also created a new background for the discussion of the relation of physics to the problems of biology." Bohr discussed the possibility that biological research may find its limits by an analogous principle of uncertainty:

> we should doubtless kill an animal if we tried to carry the investigation ... so far that we could describe the role played by single atoms in vital functions. In every experiment

> on living organisms, there must remain an uncertainty as regards the physical conditions to which they are subjected, and the idea suggests itself that the minimal freedom we must allow the organism in this respect is just large enough to permit it, so to say, to hide its ultimate secrets from us.

These statements of the famous Bohr were often confused with Jordan's ideas, and misused for supporting them (N. Bohr, 1933. *Nature* 131: 457–59). The modern developments in molecular biology allow us to be more optimistic than Bohr.

15. BACK TO CELLARS

My first university after the war was at Cologne, a city that had been 85% destroyed. The destruction of the botanical institute was exactly 100%. But I was offered the botanical garden. All its greenhouses were destroyed, and 115 bombs had made the garden resemble the landscape of the moon. However, there were cellars which were the remnants of an air raid shelter. Rats and mice enjoyed their life in these rooms.

But how to get to Cologne a few weeks after the armistice? No traveling was allowed between the four occupation zones. No mail service. Bridges had been destroyed. No railways for the public. How to come under these conditions to Cologne, how to travel around in order to find the family, how to make necessary visits to other places in order to contact colleagues? And, moreover, how to manage all these hindrances without being made a prisoner of war? A botanist has learned to handle potatoes with razor blades. That is not only good for teaching plant anatomy but also to make or to change stamps. In those days we learned how to make or to adapt certificates according to our wishes. A botanist also knows how to move in forests, how to cross rivers on rafts or by wading through at night time. Freight trains were running, carrying coal for the allied military forces, for France, etc. Why not travel sitting or sleeping on this coal? Sometimes we were lucky to find a place on the roof of a freight car. Beware of bridges! Jump down when a military patrol is coming! Climb on a car of another train! After all, one had to pay nothing for these trips; two or three days, however, were necessary to travel about 500 km. The scene suited the description in Jack London's "The Road."

In the botanical garden of Cologne there were not only those cellars. There was even a big heap of coal, no longer needed for the garden since the greenhouses were destroyed. This coal was suitable material for the black market; of course, for "official use" only (called grey market.) It enabled my gardeners to get a horse. This horse helped us to collect parts and materials from old military barracks and to build a botanical institute. The spirit of cooperation was excellent at that time. We could start teaching and doing some research work about four months after armistice. For example, the dung of the horse supplied the medium for *Pilobolus*, and thus allowed continuing research on phototropism.

The primitive conditions in those cellars still allowed R. Pohl to discover circadian rhythmicity in the phototactic responsiveness of *Euglena.* During the ensuing 30 years this phenomenon has become a worldwide favorite object in studying circadian rhythms.

My shift from Cologne to Tübingen in March 1946 was one of my illegal activities. Cologne was in the British occupation zone. The British authorities had not allowed me to move to Tübingen (in the French zone).

16. BACK TO WILHELM PFEFFER

The botanical institute in Tübingen was one of the very few in Germany which were not destroyed. Its older part was built in 1846 under the direction of Hugo von Mohl (the man whose second great contribution to biology in the same year was to introduce the term "protoplasm" in its present meaning into biology). Part of the equipment was still from Pfeffer's Tübingen time (1878–1887). There was even the book in which Pfeffer himself had noted the respective stock. I enjoyed also having about 200 square meters of garden to plant potatoes, cabbage, and soybeans. The ration tickets allowed 800 calories per day. This was not quite sufficient to survive on. The potatoes made me familiar with the potato beetle, the cabbage with the cabbage butterfly, and these insects stimulated our later research work with them on photoperiodic induction of diapause. But the soybeans preceded them in being extensively used for photoperiodic studies. In addition, planting them also as a human foodstuff had some advantage. This plant was not known to everybody in this country. There was no risk of theft. Other aspects of applied botany at that time: felling the trees in the forest (according to restricted allowances) for heating purpose, gleaning from the oat fields what the farmers had not collected with their machines.

Not to be forgotten: collecting horse and cattle dung for the potato and vegetable fields. Tübingen had no more than about 40,000 inhabitants in the first years after the war. Close to Tübingen there were villages with farmers, and also agriculture was practiced in Tübingen itself. In those years agriculture was only sparingly motorized. Almost the only impression which Goethe, during a short visit to Tübingen (1797), found worthy of mention: "the streets are extremely dirty from all that dung." What was repelling to Goethe was from 1945–1948 attractive to the university people at Tübingen (most of the other citizens of Tübingen were "natives," having their family relatives in the villages).

In Tübingen I found a place with a challenging tradition in botany. It is not only connected with Hugo von Mohl and Pfeffer, but with several other famous botanists. Here in 1694 Cammerarius discovered sexuality in plants. Correns rediscovered Mendel's laws in 1900. Vöchting made his experiments on polarity and other aspects of development physiology. Moreover, the ingenious Wilhelm Hofmeister had been working here from 1872–1877; he is the man who found the homologies in the development of mosses, ferns, and flowering plants, thus supplying an important contribution to the understanding of phylogenetic development (published eight years before Darwin's publication of *Origin of Species*). Hofmeister was a challenging person, not only for his research but also for his diligence. Before he became professor (at the age of 39) he was a bookseller, and he (a man without any academic training) had to do his microscopic work during the hours before his main business started, which meant rising at 5 A.M.

One of the important postwar aspects of the university was that many more students displayed extremely high diligence and a strong spirit of cooperation than at any time before or later. Many of the students were, of course, invalids, still wearing military clothes with the minimal necessary mending to lend a more civilian look. Research and teaching started very early. There was, for instance, the brilliant lecture by the zoologist Alfred Kühn on developmental physiology (including animals and plants). Even elder biologists and biochemists listened to this lecture (Adolf Butenandt, Georg Melchers, Anton Lang, and I). An English translation was published in 1971 (A. Kühn, *Lectures on Developmental Physiology*. New York: Springer. 551 pp.)

17. REESTABLISHING INTERNATIONAL CONTACTS

It was rather amazing to see how international contacts could be reestablished within a few years after the war. It started with the interest of the allies in learning what had been going on in several fields of science in Germany during the war. They established an "Office of Military Government for Germany Field Information Agencies Technical," resulting in a *FIAT Review of German Science 1939–1946*. Alfred Kühn and I were responsible for collecting the biology material. Perhaps the allies had expected exciting things connected with applied biology. But our reviews showed that research during the war concerned the same topics as it did before the war. Of course it was reduced to a very low minimum. I am sure that collecting this material during the years from 1945–1947 was more important to us than to the allies, because Kühn and I appreciated receiving an extra food-ration card, and sometimes the work was connected with conferences in the US headquarters at Heidelberg, where we were offered sandwiches of a quality which we never before had seen. In addition to these sandwiches, we had the opportunity to see in the headquarter's library copies of *Biological Abstracts*. I am sure that we learned more from these *Abstracts* than the allied forces learned from our *FIAT-Reviews*.

The French military government was perhaps the first to arrange contacts between their universities and ours (within the French occupation zone). For example, Gautheret introduced us to the coming age of tissue cultures. As early as 1948 I enjoyed an invitation from Eric Ashby to stay for a period of time in Manchester, and this was coupled with visits to several other English universities. These visits showed that the necessity to incorporate the "new type of plant physiologist" (see section 18 and 19) into the university was realized much earlier in Great Britain than in Germany. There was "noble" Sweden. Their "Institute for Cultural Exchange with Foreign Countries" invited quite a number of scientists from Germany to stay for a couple of months in their country. They paid us for no other obligations than to contact scientists according to our own wishes, to study in their libraries, and to buy (with an additional sum) new clothing for ourselves, food parcels for our families, etc. All this happened while food rationing was still very strong in England, and even in Sweden we had to be supplied with ration tickets.

18. THE OLD TYPE OF PLANT PHYSIOLOGISTS

The earlier plant physiologists were botanists. They demonstrated the validity of the biogenetic law: ontogeny repeats phylogeny. They repeated in their life the whole history of botany. As children they collected plants, later on they ordered them in a herbarium according to the rules of taxonomy, they continued with morphology and anatomy, and finally became interested in physiology. Only a few of these botanists were able to fill the gaps in their knowledge of physics and chemistry. This type of plant physiologist was still predominant in my country in the years after the second war. There were almost no special chairs for plant physiology, for genetics, or for general biochemistry. Otto Meyerhof was still "Privatdozent" when he received the Nobel Prize at the age of 39. Also, Otto Hahn never was offered a position in one of our universities. Biochemistry, radiochemistry, plant physiology, etc just were not scheduled in our universities. A professor of botany was expected to teach everything from taxonomy, anatomy, morphology up to physiology, and genetics (and genetics was in most cases nothing or not very much beyond explaining the Mendelian rules).

19. THE NEW TYPE AND THE COMPLEXITY OF LIVING SYSTEMS

I would not like to see the old type of plant physiologist fully disappear. But we do lack (in this country) enough scientists belonging to the new type. This is not only because leading biochemists and geneticists had to leave Germany during Hitler's time. It had already begun by neglecting Pfeffer's warning not to separate botany from the other fields of natural science. The new plant physiologist is actually what he should be in the present situation of biology: not primarily botanist or zoologist, but rather a chemist or physicist who succeeds in recognizing the physical and chemical complexity of those special natural structures which we call organisms. Most of the earlier chemists and physicists did not realize this.

Luria (in his book *Life-the Unfinished Experiment*) stated that a few decades ago certain chemists believed bacteria to be mere containers of certain enzymes and their substrates. But, looking back over the past five or six decades, perhaps each biologist has to confess that he was engaged in certain fashions of hypothesizing which were due to simplifications and frivolous generalizations of certain observations. Jacques Loeb's theory of tropisms (see section 8) is only one example.

By far more dangerous, in the twenties and thirties, was the attempt to explain many physiological phenomena on the basis of simple sol-gel transformations and changes of viscosity as they were known from chemical studies. This really became a fashion. In connection with this fashion there was the attempt to suggest pH changes as a rather general principle of explaining physiological phenomena. There was also the overestimation of the role of changes in permeability, the overestimation of regulations due to accumulation of products of photosynthesis and respiration. The discovery of auxins resulted in the fashion of explaining nearly every developmental process on the basis of auxins and antiauxins. More recently, there were (and are) the attempts at far-reaching hypothesizing on the basis of transcription and translation, or on the basis of membrane processes.

There is something in favor of each of these attempts. But the complexity had not been always fully realized. Perhaps even today we do not fully realize the inherent complexity of many biological phenomena.

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