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LEWIS JOHN STADLER

1896—1954

A Biographical Memoir by

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IN ANY FIELD of scientific research the achievements of a talented minority are largely responsible for the major advances and for the significant contributions which illuminate and determine the course and nature of future investigations. It is unavoidably true that most of us are toilers in the scientific vineyard, that at best we can do no more than add a brick here or there to the edifice of scientific theory which our intellectual superiors have erected. It is among those few with higher talents and creative powers, those whose contributions constitute the milestones of progress, that the subject of this biographical sketch assuredly belongs.

Lewis John Stadler, the second child of Henry Louis and Josephine Ehrman Stadler, was born in St. Louis on July 6, 1896. Stadler's father was brought to this country from Prague at the tender age of two years, his family having decided, following financial reverses, to try their fortunes in a new land. Life was not easy at first for the Stadler family in their adopted country and Henry Stadler went to work as an office boy at the State National Bank in St. Louis when he was but 12 years old. He remained at this bank until he retired as vice president many years later. Henry Stadler was a man of more than ordinary ability. Quiet, soft-spoken, and contemplative, he had many of the qualities which were so characteristic of his son. While still a young man, Henry Stadler married the bright and capable Josephine Ehrman, whose father was one of seven brothers of whom all but one had been rabbis. She came from a family with a real and deep appreciation of cultural and intellectual values. Lewis J. Stadler was the second child and oldest son of this felicitous union, and, according to his sister Evelyn, was adored by his mother, who felt that he was destined for greatness.

Convinced though his mother was of her son's promise, it must be admitted that his early scholastic record provided little to support her conviction. In fact, Stadler did not find himself until his post-doctorate years. As a grammar school student, he performed satisfactorily, but in high school he did not distinguish himself, ranking fifty-seventh in a class of 69 according to his own account. Talent scouts would hardly have considered him as promising scientific material. Those who knew Stadler only in his maturity, when his subtle and penetrating intellect had brought him wide recognition as an outstanding scientist, find it difficult to believe that at first he was an indifferent and lackadaisical student.

Two summer vacations during high school were spent working on farms, one in Wisconsin and one in Missouri. Apparently this contact with agriculture aroused his interest, because upon finishing high school he enrolled in the Agricultural College of the University of Missouri, where he spent his first two undergraduate years. Influenced by a family friend who suggested that knowledge of agricultural practices relating to the citrus industry might be more advantageous, Stadler transferred to the University of Florida for his junior and senior years. He obtained the degree of B.S. Agriculture from this institution in 1917. It was at Florida that he came under the tutelage of Professor W. C. Ethridge, who writes of Stadler as follows: "I first knew Lewis J. Stadler as a junior student in the scholastic year 1915-16 at the University of Florida. During that whole academic year he was enrolled in several of my classes, and these being small each member individually impressed me. I clearly remember Stadler's quiet, suave dignity, his remarkable perception, his penetrating questions, these often leading into class discussion in which he revealed a latent talent for acute analysis that was to become in later years an essential process of his mature thought. So I could, and did, say of him, 'This boy has a first class mind; he is a thinker.' Stadler in 1917, having graduated at Florida, inquired of me the conditions of graduate study and graduate aid at the University of Missouri, where I had just been appointed Chairman of the Department of Field Crops. Recalling his fine scholastic ability, I told him of graduate study here and offered him a stipend for the pursuit of it."

Thus it was that Stadler in 1917 came to Missouri to begin graduate work in the Department of Field Crops. He was awarded his A.M. degree by Missouri in the early summer of 1918 and later that summer enlisted in the Field Artillery of the U. S. Army. He subsequently obtained his commission as Second Lieutenant and was about to embark for overseas duty when the war ended. He returned for a brief stay at Missouri before spending a year (1919) in graduate study at Cornell University, where he worked under H. H. Love on biometrical problems, and to a lesser extent was associated with R. A. Emerson. It now seems more than passing strange that Stadler made a poor impression at Cornell. Emerson, who later became a great admirer of Stadler, often related how he had utterly failed to appreciate Stadler's potentialities. To Emerson Stadler gave the impression of an indifferent and negligent student with little sense of direction and purpose. It may be concluded that young Stadler was still adrift, casting about for an area of research which was intellectually appealing. He had not yet received the stimulus which would bring his undoubted abilities into focus. Following an unrewarding and unsatisfactory year at Cornell, Stadler once more came back to Missouri to finish his work for the doctorate. Even during the latter part of his graduate study he was, in scientific motivation, a lost and uncertain soul. At one time during this period he was informed by one member of his committee that he was lazy and careless and would not amount to anything if he did not change his ways. Evidently these admonitions had a salutary effect. He successfully completed his graduate work and obtained the Ph.D. degree in 1922. One may wonder if any man, who later developed into a truly distinguished scientist, ever made a more inauspicious beginning. Although, as Etheridge has indicated, his advisers were not unaware of the unusual qualities of Stadler's mind, he had yet to reveal an overwhelming passion for research; he bid fair to become one whose potentialities would never be fully realized.

Stadler's first research activities were concerned with field plot technique and related agronomic problems. In 1921 he was a joint author of two bulletins, one dealing with corn varieties and the other with productive methods for wheat. A third paper, on field plot technique, appeared in 1921. A publication on oats appeared in 1922 and one on corn in 1923. In the next two years three more articles of a purely agronomic character were published, but his first paper of a genetical nature did not appear until 1925. It may be surmised that Stadler found agronomic research interesting but not exciting. It was in the science of genetics that he was to find his metier.

Stadler became seriously interested in genetics about 1920 after reading T. H. Morgan's book, *The Physical Basis of Heredity*. From this time on, though he still was involved with more practical problems of agricultural practices, he devoted his scientific career to genetic investigations on maize. A study of variation in linkage values in maize appeared in 1925. An excellent piece of research, it attracted favorable comment and was no doubt largely responsible for his being awarded in 1925 a National Research Council Fellowship in Biology. He spent most of the 1925-1926 academic year at the Bussey Institute of Harvard University studying under Edward Murray East, and the latter part of his fellowship tenure at Cornell with R. A. Emerson. Sometime betwen his two visitations at Cornell a remarkable transformation occurred in Stadler. As a graduate student he had seemed to Emerson to be aimlessly adrift, but as a post-doctorate fellow he was a man who had charted a sure course, one who had at last found his place in the scheme of things and knew exactly what he wanted to do.

Although Stadler came to the Bussey Institute with a broad genetics program well under way and was treated as a colleague rather than as a student, he profited immensely by his contacts with the stimulating and brilliant East. Stadler, East, Albert Mangelsdorf, and Friedrich Brieger had many profitable and exciting discussions which often took place at the noon hour in a bar near the Bussey Institute. East always claimed Stadler as one of his students and Stadler freely admitted his indebtedness to the incisive East. Stadler's second stay at Cornell was in marked contrast to his first. Emerson was now greatly impressed by the purposeful drive, imagination, and originality of this former student whom he had not encouraged to remain at Cornell for graduate work. Stadler's star was now on the rise and he was well along in a career which was to bring him wide recognition. A stabilizing influence in Stadler's life was his marriage, December 18, 1919, to Cornelia Tuckerman, a fellow student at Missouri. By the time he went to work at the Bussey Institute, Stadler was the father of three children and the sobering effect of family responsibility no doubt played a part in his becoming seriously preoccupied with research.

Stadler began and ended his scientific career at Missouri. While pursuing his graduate work he was an Assistant in Field Crops (1919-1920) and then an Instructor (1920-1921). Upon finishing his thesis problem he was made an Assistant Professor in 1921. He remained at this level until 1925, when he was promoted to an Associate Professorship. In 1937 he was raised to full professorial rank. Beginning in 1930 he was employed jointly by the University of Missouri and the U. S. Department of Agriculture, a mutually satisfactory arrangement which was in effect at the time of his death. Except for a year spent at Harvard and Cornell (1925-1926) as a National Research Fellow and for a semester as Visiting Professor at the California Institute of Technology in 1940 and another at Yale in 1950, Stadler remained in residence at Missouri. Under Stadler's leadership the genetics laboratory at Missouri became a world-renowned center. Not only did Stadler bring great distinction to his school in the field of genetics, but he also created a stimulating scientific and intellectual atmosphere which made it possible for Missouri to attract able young people in related biological fields. Although he was the outstanding member of the Missouri faculty, his prestige away from his own campus was no doubt greater than at home. This should not be construed as meaning that his colleagues at Missouri were not aware of Stadler's exceptional attainments, for indeed many of them were; but Stadler led an unobtrusive life and did not play a prominent part in local campus activities. He had no formal teaching duties and consequently was not well known by the student body. It is said that more than one member of the administrative echelons at Missouri in the course of their travels was pleasantly surprised by the high esteem in which Stadler was held at other universities.

Stadler had launched an extensive program of genetical research at Missouri prior to the year spent as a fellow at Harvard and Cornell, and upon his return in 1926 continued to prosecute his investigations with unusual vigor, discrimination, and intelligence. Following his two papers on variability in crossing over (1925 and 1926), three papers appeared in 1928 on the genetic effects of X-rays in maize and barley. It is difficult to determine just when he decided to test the mutagenic effects of short wave irradiation. The first mention of his X-ray investigations appears in the 1925-1926 Annual Report of the Missouri Agricultural Experiment Station, so he must have begun these studies prior to his year as a N.R.C. fellow. However, before his experiments were fully completed, a paper by H. J. Muller appeared in 1927 announcing that exposure to X-rays greatly enhanced the mutation rate in *Drosophila*. Later, in December of the same year, at the Nashville meeting of the American Association for the Advancement of Science, Stadler gave a paper describing the effect of ionizing radiation on plants, which confirmed Muller's finding. Stadler's results were presented in 1928 in the three publications mentioned above. Muller's and Stadler's experiments were independent and coincident. The same kind of experimental work is often conducted concomitantly in more than one laboratory, and this was unquestionably true for the genetic effects of X-rays. It should be stated that Muller's experiments were more comprehensive than those of Stadler, and this was recognized by Stadler with his characteristic objectivity in his *Science* paper of 1928. To Muller rightfully goes the credit for being the first to induce germinal mutations experimentally, but it is clear that Stadler narrowly missed this honor. Yet Stadler never exhibited by word or deed any feeling of disappointment or resentment that he had in a sense been scooped. Muller and Stadler were and remained friends and each had a great admiration for the other.

The announcement that X-rays greatly increased the frequency of mutations was greeted with widespread enthusiasm. Stadler recently wrote: "The central problem of biology is the physical nature of living substance. It is this that gives drive and zest to the study of the gene, for the investigation of the behavior of genic substance seems at present our most direct approach to this problem." This sentiment was as true and as widely appreciated in the 1920's as it is today. But study of the nature of gene structure can come only by ascertaining the effects produced by new gene forms—i.e., by gene mutation. One of the difficulties in the past had been the infrequent spontaneous occurrence of gene mutations. This obstacle, at least, would be overcome if there were some method of experimentally increasing mutation rates so that larger numbers of new gene forms could be available for comparison. Immediately following the disclosure of the mutagenic effects of ionizing radiations, it was generally held that induced mutations were similar to those of spontaneous origin, and, since the rate of mutation could be greatly accelerated, the geneticist now had a new and effective weapon in his arsenal for the attack on the nature of the gene. It was the prevailing sentiment that an analysis of the wealth of mutants produced by short wave irradiation would solve the problem of gene structure. Apparently all that needed to be done was to treat as much experimental material as possible. Accordingly, many laboratories installed X-ray machines and a great deal of work on radiation effects was undertaken.

Refusing to accept uncritically the belief that spontaneous and induced mutations were identical, Stadler felt that a detailed comparison of the two kinds of mutations was essential in order to evaluate the usefulness of this new technique in determining gene structure. He conducted a long and extensive series of investigations in which he compared spontaneous and induced mutations at selected loci in maize. Stadler emphasized that the study of mutations at miscellaneous loci would be of little value because of the different mechanisms which simulate gene mutation. Such extragenic changes, which may be inherited in an orthodox Mendelian fashion, are deficiencies, duplications, small rearrangements leading to position effects, position effects involving nothing more than a recombination of genic elements by crossing over, and even the separation through crossing over of the component parts of a compound locus. To discriminate between these diverse mechanisms and that producing gene transformation is hopeless when random mutations are involved. The problem is an exacting one even when the mutational characteristics of specific loci with a variety of attributes are studied; no one realized this more clearly than Stadler, who made the first critical comparisons of induced and spontaneous mutations. The A and R alleles in maize not only affect pigment formation in various parts of the plant but their spontaneous mutation rates are high enough to yield adequate numbers of mutations for comparison in critical tests with induced mutations. From a series of extensive and beautifully executed experiments with these loci, Stadler reached the conclusion that in maize, at least, all X-ray induced mutations were extra-genic in orgin, since the kinds of changes arising spontaneously were not represented among the induced mutations. Although X-rays proved to be essentially destructive in their effects on the germinal material, some of the ultraviolet induced mutants were not associated with detectible extragenic changes; they were indistinguishable from spontaneous mutations at the A and R loci. Unfortunately, his studies on ultraviolet induced mutations were never published in full and were only alluded to in review papers.

Stadler's finding of the extra-genic nature of X-ray induced mutations was, in a sense, disappointing, since it meant that this effective mutagenic agent was of questionable value in elucidating gene structure. Convinced that knowledge of the intimate structure of the gene would come only from a detailed study of spontaneous mutants, Stadler then began a series of experiments which were in progress at the time of his death. No one was more clearly cognizant of the difficulty in showing that spontaneous mutations were not also due to extra-genic changes so minute as to escape detection by existing criteria. The facts of organic evolution would seem to demand that intragenic mutations occur. Such mutations, however, cannot be distinguished at present with certainty from other highly localized heritable variations. Stadler felt that only from a more intensive study of the mutations of specific genes could sensitive criteria be developed which would differentiate between extra-genic alterations and gene mutations. To this objective he devoted his energies to the end.

One is impressed by the design of Stadler's experiments. The answer sought was always clearly defined and the experimental approach chosen was that most likely to give unambiguous results. Stadler had a genius for selecting problems of an intrinsically simple though fundamental nature. A good example is his 1929 paper on the relation between chromosome number and mutation rate. Species of both oats and wheat have either the diploid ($2n=14$), tetraploid ($2n=28$), or hexaploid ($2n=42$) number of chromosomes. Although the mode of origin of the higher chromosome forms was unknown, there was some presumptive evidence of gene reduplication in the polyploids, since certain characters segregated in 15:1 and 63:1 ratios. Cytogenetical evidence suggested that the basic number consisted of a set of 7 chromosomes and that the gametic number in tetraploid forms contained two different sets or genomes of 7 chromosomes each, while that in the hexaploid had three different sets. It seemed probable that the chromosomes in the different genomes had many loci in common, although they had become sufficiently differentiated so that pairing rarely occurs between the chromosomes of one set and those of another. Since most induced mutations in plants are recessive, Stadler argued that if gene reduplication is common in tetraploid and hexaploid species of oats and wheat, then a much lower mutation rate should be found in the polyploid species. It would take two simultaneous mutations at homologous loci in the case of tetraploid forms and three in hexaploids before a homozygous recessive individual could arise. Diploid, tetraploid, and hexaploid species were irradiated and the selfed progeny scored for mutant types. The relatively high mutation rate in the diploid species and the progressively lower rate in tetraploids and hexaploids clearly indicated that the polyploid forms had many loci in duplicate or in triplicate. The correctness of this conclusion was later demonstrated by the convincing cytogenetical studies with wheat of E. R. Sears, who clearly showed that the chromosomes of one genome are partially homologous to specific chromosomes of the other two genomes.

Considering the comprehensive nature of Stadler's researches, his bibliography is surprisingly short, consisting of 65 papers in all, but the mere number of publications in no way reflects the impact and direction he had on genetic theory. Although his papers were not numerous, they were important and significant and invariably received wide attention. He was unsurpassed in the ability to grasp the essential and discard the trivial, to marshal the pertinent observations, and to perceive the complexities of the problem and the need for critical and decisive experiments. A masterful logician, he used a clear and persuasive style in which the arguments are presented with forensic finesse. Unfortunately a great deal of Stadler's work was never published in detail, but conclusions from unpublished studies appear in his numerous symposia papers, and for this reason these publications are among his more valuable contributions. It is here that the broad scale of his experimental work is best appreciated, and much of his influence on genetic thought stems from his participation in symposia.

Stadler's experimental studies are models in their clarity of conception and simplicity of design; he excelled as a theoretician and analyst. His powerful and subtle intellect fitted him well for the role of selecting and initiating an experimental attack on recondite problems. He was not a skillful technician, and much of the routine work was performed by others, but he kept in close touch with the day-to-day progress and he was the unquestioned leader. Stadler conducted what may be called programmatic research in that a broad and significant problem was defined and intensively studied by a research team of which he was the chief. While this experimental approach is lacking in flexibility, it enabled him to carry out successfully large-scale experiments and to arrive at definitive conclusions.

Stadler deservedly enjoyed a great prestige among his fellow scientists, and many honors came his way. He was a member of the National Academy of Sciences, the American Philisophical Society, and the American Academy of Arts and Sciences. Among the elective offices which he held were those of President of the Genetics Society of America (1938), President of the American Society of Naturalists (1953), and President of the American Association of University Professors (1932). He was active in the Society of the Sigma Xi, first serving as President of the Missouri chapter (1931), later (1934) as a member of the National Executive Committee, and finally as national President in 1953-1954. In addition to membership in the above organizations, he was a fellow of the A.A.A.S., and a member of the Botanical Society of America, the American Society of Agronomy, Phi Kappa Phi, and Alpha Zeta. During the Second World War, he served on the Scientific Advisory

Committee of the Selective Service System. He also was a member of the Postdoctoral Fellowship Board of the Atomic Energy Commission. A considerable portion of his time was spent in editorial duties; he was on the editorial board of *Genetics, The American Naturalist, Advances in Genetics,* the *University of Missouri Studies,* and *Experimental Biology Monographs.*

A clear and persuasive speaker, Stadler spoke at many national and international meetings. He was a National Sigma Xi lecturer in 1938 and gave the Spragg Memorial Lectures at Michigan State College in 1939.

Stadler had a rich, warm personality, full of understanding and sympathy for points of view different from his own. Although he held himself to exacting standards, he was tolerant of mistakes in others; his widely sought advice and counsel were never tinged with sarcasm. Intelligent, perceptive, cultured, possessing a superb sense of humor, Stadler viewed life with philosophical detachment and objectivity. He had an inner serenity which gave him a poise and suave dignity that were never ruffled by an unexpected or disappointing turn of events. A man of his intellect and scholarly aptitudes would have been successful in any field of scientific endeavor. In varied circumstances and a different environment he might well have been attracted to a career other than in genetics. Stadler was not a naturalist; he had no marked interest in plants or animals as such, but merely used them as operational integers in a search for fundamental truth. Genetics intrigued him because it dealt with the basic units of organic life, and in seeking to unravel the secrets of the gene he was engaged in a problem of the first magnitude.

Stadler had many good friends but few close ones. He was not given to demonstrative outbursts of his innermost feelings. Deeply outraged and hurt though he might be by some careless or cruel remark, his outward deportment never revealed his inward perturbation and distress. His married and family life were singularly close and intimate. The Stadlers had six children, five sons and one daughter. Theirs was a happy household, and no one who visited them could fail to be impressed by the lively and pleasant atmosphere. Two of their sons, Henry and David, followed their father's footsteps and became scientists, Henry becoming a physicist and David a geneticist.

In the late 1940's Stadler was stricken with a blood disease which was diagnosed as a form of leukemia. It then appeared that his days were numbered, but he made a miraculous recovery and seemed for several years to be in good health. His work continued with unabated interest and enthusiasm, but the disease struck again and this time there was no reprieve. In his last months he was sustained by repeated blood transfusions; when these became ineffective, his doctors decided to remove the spleen in the hope that this might prolong life. Stadler was well aware of the critical and unyielding nature of his illness, which he accepted with remarkable fortitude. He faced the inevitable courageously and calmly. In early May of 1954 he went to St. Louis to undergo a splenectomy from which he never recovered consciousness, and on May 12, 1954, the science of genetics lost one of its most distinguished men. According to his wishes, cremation took place immediately and no funeral services were held. Unobtrusively and quietly Stadler passed from this world of living men. But time can never erase from the minds of his students, friends and colleagues their memories of a wise and great man.

KEY TO ABBREVIATIONS

Amer. Jour. Bot. = American Journal of Botany
Amer. Nat. = American Naturalist
Anat. Rec. = Anatomical Record
Contr. Iowa Corn Res. Inst. = Contributions from Iowa Corn Research Institute
Jour. Amer. Soc. Agron. = Journal of the American Society of Agronomy
Jour. Hered. = Journal of Heredity
Mo. Agri. Exper. Sta. Bull. = Missouri Agricultural Experiment Station Bulletin
Mo. Agri. Exper. Sta. Cir. = Missouri Agricultural Experiment Station Circular
Mo. Agri. Exper. Sta. Res. Bull. = Missouri Agricultural Experiment Station Research Bulletin
Mo. Coll. Agri. Exten. Cir. = Missouri College of Agriculture Extension Circular
Proc. Int. Congr. Genetics = Proceedings of the International Congress of Genetics
Proc. Int. Congr. Plant Sci. = Proceedings of the International Congress of Plant Sciences
Proc. Nat. Acad. Sci. =Proceedings of the National Academy of Sciences
Rec. Genetics Soc. Amer. = Records of the Genetics Society of America
Sci. Agri. = Scientific Agriculture
U. S. D. A. Yearbook Agri. = United States Department of Agriculture Yearbook of Agriculture

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