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ERNEST ROBERT SEARS

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A Biographical Memoir by

RALPH RILEY

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BY RALPH RILEY

ERNEST ROBERT (ERNIE) SEARS was born on October 15, 1910, in the Bethel community about ten miles west of Salem in the Willamet Valley of Oregon. His parents, Jacob P. and Estella McKee Sears, were members of a large family in which teaching or farming were the principal occupations.

In his rural school at Bethel three teachers taught four grades in a single room and out of school Ernie Sears's time was mainly given to farming activities. Through 4-H Club work he got to know Oregon State College (now University), and in due course he enrolled there in the School of Agriculture. In the Farm Crops Department he enjoyed the courses on plant breeding given by Earl N. Bressman. It was Bressman who arranged for Sears to do graduate work with Professor E. M. East at Harvard in 1932. Professor East was in the Bussey Institution of Applied Biology, where Sears was also brought into contact with W. C. Castle, Karl Sax, and I. W. Bailey.

Sears left Harvard with a Ph.D. in 1936 and moved to the University of Missouri at Columbia. There he commenced work on May 1 on a USDA project concerned with polyploids under L. J. Stadler. His colleagues on the project were J. G. O'Mara and Luther Smith.

Ernie Sears' research for a period of more than fifty years, since the publication of his first Missouri paper in 1939, concentrated on wheat and its relatives. It had a coherence and an inter-relatedness that makes it hard to subdivide and make episodic. However, I have attempted to do this to understand better the totality of Sears's practical and intellectual attainments. The components that to some degree are separable are those concerned with:

- Evolution, phylogeny, and systematics of wheat and its relatives;
- Genetic structure and analysis of polyploids;
- Misdivision of chromosomes and the breakage products;
- Introduction into wheat of alien genetic variation; and
- Genetics of meiotic chromosome pairing.

This subdivision of his work was probably never in Sears' mind when he was doing the research.

EVOLUTION, PHYLOGENY, AND SYSTEMATICS

Among the earliest of Sears' works were studies of hybrids between diploid species in the Triticinae (the family in which wheat is placed), and the amphiploids derived from the treatment of these hybrids with colchicine. Papers on these subjects published in 1939 and 1941 gave considerable attention to the methodologies of colchicine treatment as well as to the relationships between chromosome pairing in the initial hybrids and the derived amphiploids. This was the origin of a lifelong involvement in the study of polyploid evolution and on the genetic and meiotic equivalences and distinctions between the chromosomes derived from different parents in the creation of allopolyploids.

At this period a very influential discovery by E. S. McFadden and Sears was that the amphiploid between *Triticum turgidum* and *Aegilops squarrosa* was phenotypically very close to *Triticum spelta*. This confirmed earlier inference from hybrids involving *Aegilops cylindrica* that the seven pairs of chromosomes (genome) in hexaploid but absent in tetraploid wheat had been derived from *Ae. squarrosa*.

I have here ascribed the wild relatives of wheat studied by Sears to the genus *Aegilops*, which was the attribution used by him at the time. Subsequently, he and Rosalind Morris (1967) accepted that the application of the rules of taxonomy required the amalgamation of *Aegilops* and *Triticum* into a common genus called *Triticum*. However, in one of the last conversations I had with Sears, in 1990, he explained that he now considered that more appropriate usage required reversion to the use of the generic name "*Aegilops*."

GENETIC STRUCTURE OF POLYPLOIDS

ANEUPLOIDS

From his earliest work, Sears strove to comprehend the cytogenetic structure of hexaploid wheat. His analysis commenced in 1939 with the study of the thirteen mature plants obtained by the pollination of two 21-chromosome haploid plants found in the *T. aetivum* (*T. vulgare* in the terms of the day) Chinese Spring. Monosomics, nullisomics, trisomics, and tetrasomics occurred either in the direct progeny of these haploids or in their derivatives. By 1944, among these derivatives, seventeen of the possible twenty-one monosomic lines had been isolated and the related nullisomics observed. Also in the 1944 study, six of the seven chromosomes of the D genome were identified and the first example of nullisomic-tetrasomic compensation was described. Nullisomics permitted definition of the chromosomal location of genes, among others for red seededness, hooding, awning, and speltoid suppression. Nullisomic III (3B) was revealed to be a rich source of monosomics for other chromosomes because of an increased level of chromosome pairing failure at meiosis.

Ultimately, this led to the formidable work that culminated in the creation of the most complete aneuploid series known in any organism. This work was crowned by the publication in 1954 of “The Aneuploids of Common Wheat” as Research Bulletin 572 of the University of Missouri, College of Agriculture, Agricultural Experimental Station. The genetic effects of each chromosome were described, in turn, on the basis of its nullisomic effects. The definition also occurred at this time of seven homoeologous groups based on nullisomic-tetrasomic compensation. Homoeologous chromosomes are those of corresponding genetic activities each derived from a different diploid ancestor of allohexaploid wheat. Recognition of the homoeologous group and the genome in which each chromosome occurred allowed every wheat chromosome to be designated with a number and a letter showing its place in the overall chromosome organization.

In “Nullisomic Analysis in Common Wheat” (*American Naturalist* 38(1953):245-52) the processes of genetic analysis are described. First is the recognition of gene absence in nulli-somics. Next is the use of distortions of the normal Mendelian segregation ratios in F2s derived from a hybrid monosomic for a chromosome carrying the dominant allele. Expression of the recessive phenotype in monosomic F1s enables the identification of chromosomes with recessive alleles. The intervarietal substitution of intact chromosomes became possible with the availability of complete monosomic series, so enabling another form of genetic analysis.

From Sears’ commitment to aneuploids arose a new structure of knowledge on homoeology and on the genetic organization of polyploid wheat.

WHEAT GENES

Not surprisingly, because of his discovery of methodologies for determining the chromosomal locations of genes, Sears used this procedure to help others with practical problems. These included identification of the genetic status of disease resistance genes—for example, in 1957 with W. A. Loegering and H. A. Rodenhiser. In addition, using chromosome substitutions, the stem rust resistance genes in Hope, Thatcher, Red Egyptian, and Timstein were positioned on nine different chromosomes. Telocentric mapping subsequently enabled *Sr9* and *Sr16*, respectively, from Red Egyptian and Thatcher to be placed about forty cross-over units apart along the long arm of chromosome 2B. Subsequently, bunt and powdery mildew resistance genes were chromosomally located.

Aneuploids also enabled Sears to contribute to the understanding of gene action in wheat. In particular, he was the discoverer of the hemizygous ineffective condition in which, when a recessive allele is carried on a monosomic chromosome, so no dominant allele is present, the recessive phenotype is not expressed. Sears explained that two doses of such recessives are necessary for gene products to pass the threshold at which the recessive phenotype appears.

Ernie Sears' astonishing discoveries show that many homoeologous genes in hexaploid wheat continue to perform essentially the same function as in the diploid ancestors from which they came. Nowadays, RFLP mapping, by and large, shows similar gene orders on homoeologous chromosomes and that, although isoenzymes may show some differences, homoeo-alleles generally still produce essentially the same proteins as each other. Genetic conservation and chromosomal stability are the principal characteristics of wheat displayed by Sears and his followers.

CHROMOSOMAL MISDIVISIONS AND BREAKAGE

For a research worker with monosomics, a concern for the misdivision of univalents was necessarily important. Sears was naturally drawn to their investigation and first reported on telocentrics and isochromosomes in 1946. He studied univalent misdivision at TI and TII of meiosis, concentrating particularly on chromosome 5A. In addition, he described the formation of isochromosomes from telocentrics and the reciprocal process. All of this was in conformity with other research on chromosome cytology of the period. However, the availability of the wheat monosomic lines enabled him to accumulate the telocentrics and isochromosomes for many different chromosomes. Consequently, by the publication in 1954 of "The Aneuploids of Common Wheat," descriptions could be included on telocentrics or isochromosomes for every chromosome of wheat complement.

By 1966 Ernie Sears could advocate genetic analysis by telocentric mapping because 42-chromosome lines, with one chromosome represented by a telocentric in the disomic condition, were available for every chromosome of the wheat complement. Mapping determined the frequency of crossing over between a genetic locus and the centromere.

Ernie Sears' wife, Lotti Steintz-Sears, had been a major collaborator with Ernie in this work on misdivision products, and by 1974 and 1978 they were able to report on the availability of an almost complete set of twenty-one 44-chromosome lines in which every wheat chromosome was represented by a pair of telocentrics for both arms of the chromosome. This was a quite astonishing achievement requiring perseverance and dedication to create plant material of enormous benefit to wheat geneticists.

ALIEN GENETIC VARIATION

About the time that Sears worked on interspecific hybrids between 14-chromosome species related to wheat and published his first study on aneuploids, J. G. O'Mara in Missouri was researching wheat-rye hybrids, triticale, and wheat-rye chromosome addition lines. O'Mara's work was done over the period of the late 1930s to the early 1950s. I do not know how scientific responsibilities were shared at that time, but Sears did not turn to wheat-rye combinations until some time after this period. Instead, he produced in 1953 hexaploid wheat forms to which were added the 7-chromosome haploid complement of *Haynaldia villosa.* Remarkably this was achieved by hybridizing *T. dicoccoides (2n=28) x H. villosa (2n=14)* and by top crossing the hybrid with *T. aestivum* and backcrossing to *T. aestivum.* Subsequently, Beale Hyde used this material to make wheat lines in which, in turn, every chromosome of *Hynaldia* was separately added to wheat.

At the 1956 Brookhaven Symposium, Sears described remarkable work in which leaf rust resistance of *Aegilops umbellulata* was transferred to common wheat. This commenced with the addition to *T. aestivum* of a single chromosome of *Ae. umbellulata* that caused rust resistance. The added chromosome also produced economically disadvantageous modifications to the phenotype of *T. aestivum.* Consequently, if the rust resistance were to be made available for wheat improvement, the determinant of resistance had to be disassociated from other deleterious genes on the chromosome. Using entirely innovative techniques, Sears X-rayed plants of wheat to which was added an isochromosome of the resistance-determining arm. The irradiated plants were used to pollinate normal wheat and resistance progeny were selected. Forty of these had one of at least seventeen different translocations between the *Aegilops* chromosome and wheat chromosomes. There was one line with the resistance chromosome segment apparently incorporated in the form of an intercalary translocation. The line had normal pollen transmission and was not detectable cytogenetically. Further work, published in 1966, showed that the *Ae. umbellulata* segment was not in an intercalary position but that a long *Aegilops* segment had replaced the terminal part of the long arm of wheat 6B. Undoubtedly, the absence of significant deleterious effects was related to the homoeologous relationship between the *umbellulata* segment introduced and the 6B segment removed. The alien leaf rust resistance introgressed with wheat in this way has been of considerable economic significance. A remarkable new technology had been created that was subsequently used in several laboratories outside the United States to incorporate other forms of alien disease resistance into wheat.

The notion that bibrachial chromosome could be created from the fusion of telocentrics of different, even unrelated, chromosomes was proposed by Jack (J. W.) Morrison in 1954, and several apparent examples were described by Muramatsu and Sears in 1969. However, all of them might have been explained alternatively as having arisen by homoeologous recombination. To evaluate this, Sears set up an experimental situation in which chromosomes 6B and 5R were simultaneously monosomic and showed that bibrachial chromosomes with one 6B and one 5R arm were produced with a frequency compatible with the separate likelihoods of simultaneous misdivision in each univalent. This validated the potential usefulness of centric fusion in breeding when deletion of a wheat chromosome arm is not phenotypically severe and where the added alien arm does not incorporate deleterious genes as well as the beneficial gene.

By 1971 Sears was able to report on the isolation of every chromosome of Imperial rye as a separate addition line to Chinese Spring, so completing work the first stages of which had been reported in 1958. Thus, Sears took over and completed for the USDA the investigation initiated by J. G. O'Mara in 1940.

GENETICS OF MEIOTIC CHROMOSOME PAIRING

One of the discoveries that wheat chromosome 5B has genes that affect chromosome pairing at meiosis was made in Sears's laboratory by M. Okamoto. Ernie Sears encouraged the work of Okamoto on these genetic systems. Subsequently, also in his laboratory, the work of Moshe Feldman resulted in proposals about the processes by which the *Ph* locus on chromosome 5B confines meiotic pairing to fully homoeologous partner chromosomes.

Although involved in the encouragement of work of this kind and as a frequent commentator on the genetics of chromosome pairing, Sears' direct involvement has principally concentrated on attempts to mutate the *Ph* locus. After considerable research, in 1977 Sears was able to report on the production of a viable mutant that appeared to be a deficiency for the *Ph* locus, on 5B, or in which the locus was rendered ineffective. I will rehearse some numbers from this work because they indicate the scale and patience that characterized Ernie Sears' work. X-irradiated euploid pollen was applied to previously emasculated spikes of *T. aestivum* plants monosomic for a genetically marked chromosome 5B. One thousand two hundred seventy-eight offspring were obtained, of which 675 were immediately eliminated because they carried the marked chromosome 5B or because they were clearly nullisomic for 5B. Those with the marker would not display any mutation to recessive that had occurred in the irradiated 5B chromosomes. Four hundred thirty-eight of the retained offspring were tested for changes in the regulation of pairing. One mutant was isolated that was apparently deficient for the *Ph* locus. This mutant, designated *ph1b*, could be made homozygous and, although somewhat reduced in vigor and fertility, has proved to be useful in breeding and research. The persistence and perseverance that were regularly part of Sears' work are well revealed by this example—namely, pollinate hundreds of spikes, search through an initial 1,278 offspring to find one mutant, and use markers to simplify the task.

CHINESE SPRING

No tribute to Ernie Sears could omit a mention of Chinese Spring, the variety that, as a result of his work, has become the reference base for all wheat cytogeneticists. Sears and T. E. Miller have reported on this. Chinese Spring was the variety in which Sears first obtained the two haploids that were the origins of the aneuploids. The haploids arose in work on wheat-rye hybrids being used to test for chromosome doubling by heat shock. Chinese Spring was used because of its ready cross-ability with rye. It appears that the variety originated in Szechuan, China, and traveled via Cambridge, England, to North Dakota and Saskatoon, Canada, and then to Columbia, Missouri, before being used by Sears.

Although the use of Chinese Spring is often scorned by breeders, it has without doubt made possible an explosion of scientific knowledge about wheat.

A CAREER IN WHEAT SCIENCE

All who followed Sears' work and benefited from it will acknowledge the characteristics that pervaded it for more than five decades. They were intellectual rigor, experimental flair, cytogenetical insight, precision of communication, desire to collaborate, and extreme generosity with plant material and ideas. No matter how close or remote geographically any wheat cytogeneticist was to Ernie Sears all are in his debt.

Sears enjoyed the loyalty of the Missouri Agricultural Experimental Station and the University of Missouri, Columbia, for more than five decades. He returned it equally because he felt that Columbia was the place where he could work most effectively and comfortably. During his time at the university in Columbia, he was clearly much influenced in the first instance by L. J. Stadller. Among his many other distinguished colleagues were Alex Faberge, Melvin Green, Jack Shultz, George Sprague, A. P. Swanson, and Barbara McClintock. In his wheat group for varying periods of time were Moshe Feldman, Bill Loegering, Tris Mello-Sampayo, K. Tsunewaki, Gordon Kimber, Bikram Gill, Bob MacIntosh, Henry Shands, M. Okamato, M. Muramatsu, and Beale Hyde. While working collaboratively with these colleagues, and certainly greatly influencing their work, often his name did not appear on the papers that emerged. Ernie Sears was a modest person, even self-deprecating. His self-deprecating humor showed up in a conversation I had with him after dinner at my home in Cambridge, England, in 1958. In describing his home in Columbia, Missouri, Sears said, "Yes, I have a back yard. I planted 1,000 pine; 990 died."

His joy was the wheat plant and its relatives. It was rare for him to work on any other organism. The value of his work was widely recognized and brought him many well-deserved honors. Among these was the Hoblitzelle Award for Research in Agricultural Sciences. This $10,000 enabled him to buy his attractive home in Columbia, which characteristically he called "Mob Hill." Here he raised his happy family of three children by his second wife, Lotti Steinitz-Sears—John, a medical student; Barbara, now widowed and associate professor of botany and plant pathology at Michigan State University; and Katie, now married and living in Minneapolis. Mike, the son of his first wife Caroline, is now director of the Cloverwork Foundation.

Sears remained very fit right up to his death, playing tennis and badminton and cutting his four acres of grass at Mob Hill with only a motorized push mower. He was unflappable and simultaneously generous and frugal, the epitome of a hands-on scientist. He had the minimum of technical assistance—potting his own plants, watering them, making his own pollinations and slides, and harvesting and meticulously storing the seeds of an enormous collection of genotypes. It was only in this way that Sears felt he thoroughly understood his material and was able to "treasure his exceptions." The way E. R. Sears dedicated himself to a very specialized branch of science is an example to us all.

HONORS AND DISTINCTIONS

ACADEMIC DEGREES

1932 B.S., Oregon State College
1934 M.A., Harvard University
1936 Ph.D., Harvard University

HONORARY DEGREE

1970 D.Sc., Göttingen University

AWARDS

1951 American Society of Agronomy, Stevenson Award
1958 Gamma Sigma Delta National Award for Distinguished Service
Hoblitzelle Award for Research in Agricultural Sciences
1970 Sigma Xi Research Award
1973 Oregon State University, Distinguished Service Award
1977 Genetics Society of Canada, Excellence Award
1980 Hard Red Winter Wheat Workers, Wheat Science Award
1981 National Agribusiness Association, Agricultural Science Award
1983 Missouri Academy of Science, Scientist of the Year
1986 Wolf Prize in Agriculture
1990 University of Missouri, Curators Award for International Service

USDA AWARDS

1958 Superior Service Award
1980 Distinguished Service Award
1987 Science Hall of Fame

LEARNED SOCIETIES

National Academy of Sciences (1964)
American Academy of Arts and Sciences (1953)
Genetics Society of America (President, 1978-79)
American Society of Agronomy (Fellow)
Botanical Society of America

American Society of Naturalists
American Association for the Advancement of Science (Fellow)
American Institute of Biological Sciences
Genetics Society of Japan (Honorary)
Indian Society of Genetics and Plant Breeding (Honorary)
American Association of Cereal Chemists (Honorary)

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1948

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1953

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1954

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1956

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1957

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1958

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1962

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1966

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1968

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1973

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1975

An induced homoeologous—pairing mutant in *Triticum aestivum. Genetics* 80:74.

1976

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1977

An induced mutant with homoeologous pairing in wheat. *Can. J. Genet. Cytol.* 19:585-93.

1978

With L. M. S. Sears. The telocentric chromosomes of common wheat. *Proceedings of the Fifth International Wheat Genetics Symposium*, vol. 1, pp. 389-407.

1981

With W. Q. Loegering. Genetic control of disease expression in stem rust of wheat. *Phytopathology* 71:425-28.

1982

A wheat mutation conditioning an intermediate level of homoeologous pairing. *Can. J. Genet. Cytol.* 24:715-19.

1985

The transfer of short segments of alien chromosome to wheat. In *Advances in Cytogenetics and Crop Improvement*, eds. R. B. Singh, R. M. Singh, and B. D. Singh, pp. 75-79. Ludhiana: Kalyani Publ.

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