HISTORY

Founder of Modern Wheat Genetics

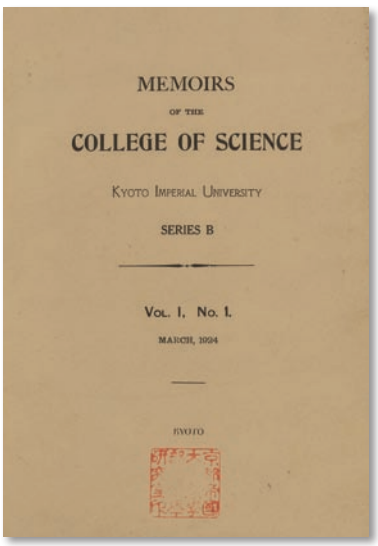
The Legacy of Professor Hitoshi Kihara

Dr. Hitoshi Kihara, professor emeritus of Kyoto University was born in Tokyo in 1893, and spent his undergraduate and graduate years in Sapporo, Hokkaido. He often said that he was raised in the wilderness near the Ishikari River. This upbringing seems to have given him a sturdy naturalist's spirit, which influenced his whole life.

IN 1920, when Kihara was a graduate student at Hokkaido Imperial University, Professor Kan Kōriba of the College of Science of Kyoto Imperial University (the former name of Kyoto University) appointed him as one of his assistants. Four years later, Kihara submitted a doctoral dissertation to the College of Science, and received his science doctorate in 1924. In the same year, his dissertation was published in the Memoirs of Kyoto Imperial University's College of Science (*Series B*, **1**, 1–200). The article established a basis for genome analysis, and Kihara was proud to have it published as a lead article in the first volume of the college memoirs. It was to become one of his top three most widely cited scientific publications.

Prior to the Kihara's work in 1924, Sakamura (1918) determined the chromosome numbers of eight different wheat (*Triticum*) species, finding 2n (somatic chromosome number) =14 for one species, 2n=28 for four species and 2n=42 for three species. Those findings led Sakamura to discover polyploidy in wheat, with the basic chromosome number (x) of seven; the diploid species being $2n=2x=14$, tetraploids $2n=4x=28$ and hexaploids $2n=6x=42$.

In 1918, following on from Sakamura's work, Kihara analyzed the meiotic chromosome behaviors of $3x$ hybrids obtained by $2x \times 4x$ wheat and $5x$ hybrids obtained by $4x \times 6x$ wheat. In his 1924 dissertation, Kihara reported their chromosome pairings: 7 bivalents + 7 univalents in the $3x$, and 14 bivalents + 7 univalents in the $5x$ hybrids. Those results led him to conclude


MEMOIRS
OF THE
COLLEGE OF SCIENCE
KYOTO IMPERIAL UNIVERSITY
SERIES B
VOL. I, NO. 1.
MARCH, 1924
KYOTO


MEMOIRS OF THE COLLEGE OF SCIENCE, KYOTO IMPERIAL UNIVERSITY, SERIES B, VOL. I, ARTICLE 1.

Cytologische und genetische Studien bei wichtigen Getreidearten mit besonderer Rücksicht auf das Verhalten der Chromosomen und die Sterilität in den Bastarden.

Von

HITOSHI KIHARA.

Mit 5 Tafeln und 117 Textfiguren.

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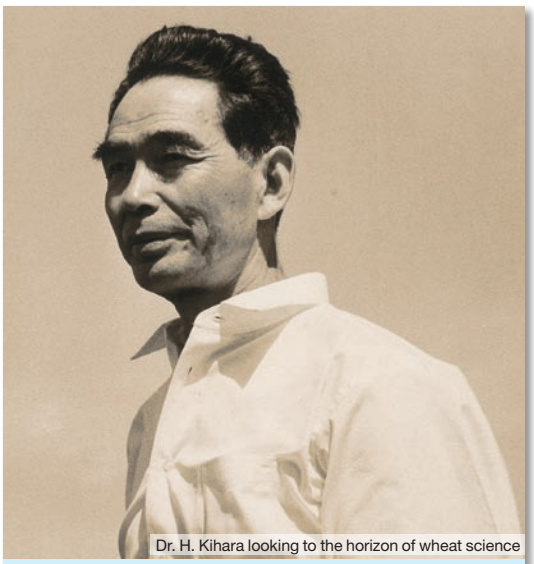
Front cover of *The Memoirs of the College of Science, Kyoto Imperial University, Series B*, **1**(1), 1924, and the first page of Dr. Kihara's article, which appeared on pp.1–200.

that $2x$ and $4x$ wheat have one set of seven chromosomes in common and the second set of $4x$ wheat is unique, and that the $4x$ and $6x$ wheat have two chromosome sets in common and the third set of $6x$ wheat is different from the former two. From those conclusions, Kihara considered the set of seven chromosomes as a genetic unit of inheritance, and gave it the name "genome" (Kihara 1930). He designated the genome formulae, AA, AABB, and AABBDD, to the diploid (= einkorn), tetraploid (= emmer) and hexaploid (= common) wheat, respectively. Kihara and Lilienfeld (1934) later discovered a new $4x$ species, to which they designated the genome constitution AAGG: the completion of genome analysis of the *Triticum* genus. Kihara's school then extended genome analysis to several other gramineous genera, such as *Aegilops* (F. A. Lilienfeld, S. Matsumura, M. Tanaka), *Avena* (I. Nishiyama), and *Echinochloa* (T. Yabuno) (the main workers are indicated in parentheses).



Dr. H. Kihara looking to the horizon of wheat science

Hitoshi Kihara (1893 - 1986) was a geneticist served as a professor at the Faculty of Agriculture, Kyoto University from 1927 to 1956. He was elected a member of the Japan Academy. He noticed that in wheat seven chromosomes form a basic unit of the inheritance and function, and thus named it genome. The concept of genome formed the basis for development of biology and genetic engineering.

The genome analysis of wheat revealed that its A genome originated from $2x$ wheat (Kihara 1924). The origin of the second genome, B, is still in debate, although several studies indicate *Aegilops speltoides* as the probable donor of this genome.

Genome analysis of the genus *Aegilops* revealed that a $4x$ species, *Ae. cylindrica*, has a CCDD genome constitution, and a $2x$ species, *Ae. caudata*, has a CC genome (Kihara and Matsumura 1941). Kihara thought the following two equations should hold true for the main characteristics of emmer and common wheat and for *Ae. caudata* and *Ae. cylindrica*:

(i) [Common wheat (AABBDD)] – [Emmer wheat (AABB)] = [D-genome donor]

(ii) [*Ae. cylindrica* (CCDD)] – [*Ae. caudata* (CC)] = [D-genome donor]

If the results of the two equations were the same, the characteristics derived from them should be the characteristics of the D-genome donor. Kihara observed seven characters of all four species, finding that the characteristics suggested by the two equations coincided with each other on six characters as follows: the number of 2n chromosomes is 14, there are spike breaks in the umbrella type, the empty glume is awnless with flat top edge, the outer glume of the lateral spikelet has a short awn, and the empty glume does not have keel. He searched for his *Aegilops* collection, and found that *Ae. squarrosa* possessed all of those characteristics. He submitted a full-sized article to report those results to a Japanese journal, but it was not published due to the difficult economic situation at the end of World War II. Instead, a manuscript of two printed pages in Japanese was published in 1944 in a Japanese journal called *Agriculture and Horticulture*. The article was titled "Discovery of the DD-analyser, one of the ancestors of *Triticum vulgare*." It was to become the most frequently cited of all his written works.

In 1955, after the end of World War II, Kyoto University organized its first full-scale overseas expedition called the Kyoto University Scientific Expedition to the Karakoram and Hindukush

Members of the Kihara School celebrate his 50th year of wheat research. Dr. Kihara invited the students to the Nishiatami Hotel on 22 November 1968. He named the gathering the *Triticum* 50 Celebration (in Chinese characters: 採而来50祝賀会).

(KUSE). Kihara led the expedition, which comprised two teams: the Hindukush team, headed by Kihara, and the Karakoram team, headed by Kinji Imanishi〔For more information: *Research Activities*, **3**(4), 4-6〕. The two teams comprised twelve members, one reporter, and two photographers in all. They left from Tokyo Airport on 14 May 1955, and returned on 3 September. Kihara's main mission was to complete a field survey of the Fertile Crescent and its neighboring regions, where common wheat was assumed to have originated. The results of this expedition were published in eight volumes, the first of which was titled *Cultivated Plants and their Relatives*. The volume's nineteen chapters dealt with fourteen types of cultivated plant, covering twenty-one genera and thirty-four species in all. Later, the members of KUSE and their coworkers in Kihara's and related schools at Kyoto University became widely recognized as specialists in economic plants. This group of specialists included K. Yamashita, S. Nakao, M. Tanaka, S. Sakamoto, N. Yamamoto and K. Fukui, and the Faculty of Agriculture came to be known as "the Faculty of Expeditions."

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In the early 1950s, Kihara's main interest shifted to interaction between the genome and plasmon (cytoplasmic genome). He developed a method of studying this problem called "nucleus substitution," a process which involved repeated backcrosses of the hybrid between the plasmon donor as the female and the genome donor as the recurrent pollen parent. The method was based on their different transmission modes: biparental transmission of the genome and maternal transmission of the plasmon. Kihara transferred the *Ae. caudata* plasmon to common wheat using this method. The alloplasmic wheat thus produced expressed pollen sterility, leading to the discovery of the first case of cytoplasmic male sterility in wheat (Kihara 1951). This article describing this process, titled "Substitution of the nucleus and its effects on genome manifestation" became one of Kihara's three most frequently cited articles, launching the new field of hybrid wheat breeding.

Kihara's school extended plasmon analysis to most species of the *Triticum-Aegilops* complex. Plasmons were introduced to a dozen of the representative types of wheat, and were classified by their effects on wheat phenotypes and the molecular differences in their organellar DNAs (Fukasawa 1953; Tsunewaki *et al.* 1996, 2002), along with complete sequencing of the chloroplast and mitochondrial DNAs of common wheat (Ogihara *et al.* 2002, 2005). In combination, Kihara's genome analysis and Tsunewaki and his colleagues' plasmon analysis established the maternal and paternal lineages of all *Triticum-Aegilops* species.

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Kihara is one of the discoverers of the sex chromosome in plants, finding it in *Rumex acetosa* (Kihara and Ono 1925). Later, he bred seedless autotriploid watermelon, and in 1952 was honored with the Award of the American Society for Horticultural Science. In 1953, Kihara served as vice-president of the 9th International Genetics Congress in Bellagio, Italy. He was elected chairman of the 1st International Wheat

Dr. Kihara's 1946 dictum
English version (left) and original (right)

Genetics Symposium, held in Winnipeg, Canada in 1958. He delivered the symposium's opening address, and in its closing session, he left a deep impression on the assembled scholars with a lecture incorporating color films of KUSE.

Kihara's school would later produce leading geneticists in the fields of molecular and population genetics, including H. Ozeki, T. Yura, and N. Sueoka in molecular genetics, and K. Kojima, M. Nei, T. Ohta, and T. Mukai in population genetics.

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Kihara was an enthusiastic sportsman who enjoyed playing baseball, tennis, and particularly skiing. The first book he wrote was about skiing—a volume coauthored by K. Endo that was published in 1919. He was the first Japanese official to attend the International Ski Tournament held in Finland, attending the 9th tournament in 1926, during which Japan was formally approved as a member of the International Ski Federation. He served as the leader of the Japanese ski team in two Winter Olympic Games: the 8th, held in Squaw Valley, USA, and the 9th, held in Innsbruck, France. He was also active in the field of nature conservation. From May 1955 to March 1969, while he was director of the National Institute of Genetics in Mishima, Shizuoka, he was engaged in efforts to conserve the natural flora of entire area of Nishikidani Valley. The valley is the water source of the Kanogawa River, which was used to irrigate the Tagata Plain in Shizuoka Prefecture.

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Kihara's originality is clearly evidenced by the quantity of his works involving pioneering first achievements and discoveries. He was a man who constantly spoke about his future plans—always looking forward. He did not preach his philosophy to his students, nor direct them towards their future. Nevertheless, they were greatly influenced through their dialogues with his Kihara, and the pride that they took in being his students, was evident when they formed a group known as "Kihara's School."

The following dictum of Kihara is well known among biologists in Japan and around the world to this day:

> *The History of the Earth is recorded in the Layers of its Crust; The History of all Organisms is inscribed in the Chromosomes.*
>
> ***Hitoshi Kihara, 1946***

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Acknowledgements Dr. Kihara's writings, including *Wheat—Records of a Biologist* (written in Japanese), Chuokoronsha, Tokyo, 1951, and *Wheat Studies—Retrospect and Prospects*, Elsevier Scientific Publishing Co., Amsterdam, 1982, were referred to in writing this article. The information generously provided by Miss Y. Kihara is also gratefully acknowledged.