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 Kōhiba 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 × 4x wheat and 5x hybrids obtained by 4x × 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...
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).

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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.

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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
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(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.”

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.

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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
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.

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.

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

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.