Perspectives

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HITOSHI KIHARA, Japan's Pioneer Geneticist

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The history of the earth is recorded in the layers of its crust; the history of all organisms is inscribed in the chromosomes.

THIS striking aphorism, engraved in a bronze relief at the Kihara Institute in Yokohama, was coined by KIHARA in 1946. It has a remarkably modern ring; replace chromosomes by DNA and it could have been written today.

HITOSHI KIHARA was born in Tokyo on October 21, 1893 and died on July 27, 1986 at the age of 92. Were he alive today he would be starting his second century. During his long research career–some 65 years–his main interest was the genetics of wheat, but his versatility and wide-ranging curiosity led him along many paths.

KIHARA went through grade school and high school in Tokyo. Then, because he didn't conform to the highly competitive custom of aiming for high grades and essaying difficult entrance examinations, he did not enter the prestigious Imperial Universities of Tokyo or Kyoto. Instead, he went to far-off Sapporo on Japan's Northern Island to enroll at Hokkaido University. In a biographical note he mentions a brilliant but late-blooming physicist and then says of himself that "I did not so much mature late but rather matured hardly at all." In a sense this is true, for throughout his life he retained a small boy's curiosity about everything.

In 1918 the pioneer Hokkaido wheat geneticist, TETSU SAKAMURA, had just cleaned up a cytogenetic morass by determining the correct chromosome numbers for different wheat varieties. He identified diploid, tetraploid, and hexaploid varieties with zygotic chromosome numbers 14, 28, and 42, and made crosses among them. KIHARA's entry into wheat genetics was through the cultivation of a pentaploid hybrid. Interrupted by a year in the army, he resumed his work in Hokkaido and in 1921 transferred to Kyoto University. This was the beginning of 35 highly productive years there. Ultimately, he was to author more than 400 papers and 20 books.

It was KIHARA's good fortune to receive SAKAMURA's entire collection of wheat stocks. In 1918 SAKAMURA was promoted to the Chair of Plant Physiology, entailing two years of study in Europe. He never returned to his wheat work, one more example of being promoted out of a promising scientific career. KIHARA never failed to acknowledge his indebtedness to SAKAMURA and dedicated his major book (KIHARA 1982) to him. It is this chance circumstance that led to KIHARA's paradoxical emphasis on wheat in a rice-growing country. He did, however, do several studies on rice and its ancestry, and on other grains, but these were minor relative to his monumental studies of wheat.

At the time of KIHARA's appointment in Kyoto, a potential faculty member was required to spend two years abroad in order to qualify for a position at an Imperial University. A personable, adventurous, ambitious, and intellectually curious young man, KIHARA made the most of his opportunities abroad. The bulk of his time was spent at the Kaiser Wilhelm Institut in Berlin-Dahlem, working with C. CORRENS, one of the three who rediscovered MENDEL's laws. KIHARA also met the other two, VON TSCHERMAK in Austria and DE VRIES in Holland. In Russia he visited KOLTZOV and KARPECHENKO, but missed his counterpart VAVILOV, who was away. Later, the two men met in Japan. They shared a deep interest in the wild relatives of cultivated plants, and both organized extensive expeditions to discover them. On the way back to Japan, KIHARA visited Columbia University in New York, meeting T. H. MORGAN and E. B. WILSON. While in Germany, he sharpened his cytological skills in chromosome studies of *Rumex acetosa* and several other species of sorrel. Among other things, he determined chromosome numbers and described *X* and *Y* chromosomes

This essay is dedicated to MOTOO KIMURA in honor of his 70th birthday. He was responsible for my getting acquainted with KIHARA

FIGURE 1.—HITOSHI KIHARA.

FIGURE 2.—KIHARA while he was studying in Germany.

in sorrels. He was thus one of first to find sex chromosomes in angiosperms.

Returning to the University of Kyoto, he remained there until 1955. During this time Kyoto became a world genetics center, and KIHARA was soon the best known geneticist in Japan. Although there were severe hardships during World War II and work was greatly inhibited, his research did not stop. Reaching retirement age in 1955, he became director of the National Institute of Genetics in Mishima, retiring a second time in 1969. He continued research for the rest of his long life in Yokohama in his own Institute for Biological Research.

From hybridization of polyploid wheat varieties, KIHARA discovered that only those with a multiple of seven chromosomes were normally viable, and only those with 14 or a multiple of 14 were fully fertile. He adopted WINKLER's newly coined word, "genome," designating the basic monoploid chromosome set, but he gave it a functional meaning as the minimum set containing all the essential genes. By studying the cytology of meiosis, he confirmed the irregular assortment of univalents in hybrids with an odd ploidy level, in contrast to orthodox segregation in those with an even number of genomes.

KIHARA soon realized that the degree of meiotic synapsis could be used as an index of similarity and relationship, and designated the three main wheat genomes as A, B, and D. Thus, diploid einkorn wheat (*Triticum monococcum*) is AA, tetraploid emmer (*Triticum dicoccum*) is AABB, and hexaploid bread wheat (*Triticum aestivum*) is AABBDD. A fourth genome, the G group from *Triticum timopheevi*, was added later. One of KIHARA's outstanding discoveries was the ancestry of bread wheat. Having identified the D group from genome analysis, he suspected that the key to wheat ancestry lay in the Middle East. Going there, he found diploid DD goat grass (*Aegilops squarrosa*) growing as a weed in tetraploid emmer AABB wheat fields. In his words, "This observation opened our eyes to the possibility that if *Aegilops squarrosa* (2x) grew as a weed in an emmer (4x) wheat field, the two different grains might very well produce a hybrid (3x) and in the next generation join to generate the bread wheat 6x." He proceeded then to construct such a hexaploid and found that it was completely fertile with cultivated bread wheat and the chromosomes paired perfectly. Thus the whole story–sympatric growth of parental species, hybrid formation, production of unreduced gametes, and union of these gametes to produce a hexaploid–was confirmed (TSUNEWAKI 1989). During the 20-year period starting in 1930, KIHARA determined the genome composition of all known wheat and goat grass species.

While KIHARA was determining the ancestry of wheat in Asia, ERNEST SEARS was making the same discovery at the University of Missouri. Sears had admired KIHARA's work since his student days in the 1930s. He recalled that during World War II he dreamed of being shot down over Kyoto, being forced to parachute, and hoping he could find KIHARA and be welcomed as a fellow cytogeneticist. The two never met until KIHARA's trip to the United States in 1951, the first postwar visit by a Japanese geneticist (SEARS 1987).

KIHARA's trip to Pakistan, Afghanistan, and Iran was widely publicized in Japan, and a documentary film, *Karakoram*, was shown throughout the country. His name was well known to the Japanese populace. An important spin-off from these trips was a large collection of wild relatives of various cultivated plants, material that has been of use to many plant breeders. Along with VAVILOV, he played a major role in popularizing this now-common practice.

In 1951 KIHARA found cytoplasmic male sterility in several varietal and species crosses. He was able to identify both the cytoplasmic sterility factors and the specific nuclear restoring genes. Needless to say, this work, reported at the International Congress of Genetics in Montreal in 1958, attracted a great deal of attention from companies interested in developing hybrid wheat. As the preeminent wheat geneticist, KIHARA was the founder and first chairman of the International Wheat Symposium in 1958. He attended the regular meetings at five-year intervals, his last being in 1983. At age 90 he addressed the group and discussed the origin of "Daruma," a variety that has provided genetic material for many of the semi-dwarfs that have been so important in the green revolution. Daruma is a folk figure to which foreign visitors are often introduced in the form of a roly-poly seated doll. The custom is for Daruma to have only one eye at the beginning of a conference; if the meeting is successful, the second eye is painted at the conclusion. Using this name for the wheat is especially appropriate, for the Daruma doll recovers its upright posture when tipped; a striking feature of semi-dwarf wheats is that they remain standing after strong winds and heavy rains.

Although wheat was KIHARA's main interest throughout his working life, it was by no means his only one. As mentioned earlier, he was one of the first to identify sex chromosomes in flowering plants. He developed several methods for producing haploids. He had interest in rare plants and living fossils. Another interest was variegation, including that found in historical writings. And, as expected of Japan's leading geneticist, he also studied rice and its origins. His early work in 1918 provided the technique and incentive for studying polyploidy in other crop genera, and he himself discovered a polyploid series in oats.

KIHARA was an early advocate of polyploidization as a tool in plant breeding. Noting that many domestic varieties (such as oats, wheat, and strawberry) are polyploid, he argued that this should become a regular part of plant breeding technology. This was a far-sighted suggestion, later becoming routine after the discovery of colchicine and other chromosome-doubling treatments.

He also recognized the desirability of seedless varieties of edible plants, such as bananas, grapes, and pineapples. The explanations are diverse. Pineapples, for example, are self-incompatible, so that clones of vegetatively propagated and therefore identical plants are seedless. KIHARA was especially interested that vegetatively propagated, cultivated bananas are triploid while their wild relatives with seeds are diploid. So he decided to construct a seedless triploid watermelon. He started in 1939, first obtaining a tetraploid from a normal diploid by colchicine treatment. Then, using pollen from a diploid on a tetraploid stigma (the reciprocal mating didn't work), he got triploid progeny. As expected, these did not produce seeds; but without pollination they didn't produce melons either, and triploid plants did not produce appreciable amounts of functional euploid pollen. So he grew diploid plants in the same field to supply the needed pollen. But the only way to distinguish seeded from seedless melons was to cut them open. Simple Mendelism came to the rescue. KIHARA used a color-pattern gene to distinguish diploids from triploids. Seedless watermelons attracted a great deal of attention in Japan, and KIHARA became almost as well known for this as for his collecting expeditions. The melons also attracted attention elsewhere, and in 1952 the American Society of Horticulture gave KIHARA its annual award for this work.

Another of KIHARA's interests was the direction of spiraling in such places as flowers, spikelets, and climbing vines (KIHARA 1982). He collected data from the literature and from the field, and performed various experimental and genetic tests. For example, in alfalfa the direction was a simple Mendelian trait. KIHARA forced some vines to coil in the wrong direction, producing bizarre shapes that clearly showed the frustrated plant's attempt to do what its genes told it to do. Typically, his curiosity went beyond biology and he made historical studies such as examining the direction of coiling of ropes in Japanese history. Because of his interest in spiraling he noted things that most of us overlook. I remember the delight with which he showed me a painting by a European master in which a rope changed its twist from right-handed to left-handed as it went through a pulley. He was also surprised to find wrongly coiled DNA diagrams in about a fourth of the genetics textbooks he examined, including–much to his amusement–a diagram in JIM WATSON's book.

KIHARA had a life-long interest in athletics. As a student he was active in many sports. His book of photographs (KIHARA 1985) shows him involved in baseball, archery, racing, and javelin throwing. He was a skilled skier and traveled with the Kyoto University Alpine club to the snowy heights of Japanese mountains. The group planned to climb K2, but World War II intervened. Later, KIHARA led the Japanese ski team at the Winter Olympics in 1960 and 1964.

His interest in archery led to a fascinating paper (reprinted in KIHARA 1982) on the traditional contest in an ancient Kyoto temple, Sanjusan-gendo. The archer sat on a small box at one end of a 120-meter veranda, and the object was to shoot as many arrows as possible to the other end in a 24-hour period. Only those arrows that traveled the entire distance in the air counted. An assistant handed bamboo arrows as fast as they were shot. The record was 8,133 out of 13,053 attempts, or an arrow every 6.6 seconds. Shooting an arrow every 6.6 seconds for 24 hours seems an almost unbelievable feat of endurance. The training was long and arduous. This record, set in 1686, was never equaled, and the games finally stopped with the Meiji restoration nearly 200 years later. A visitor to the Sanjusan-gendo can still see marks on the rafters made by misdirected arrows. KIHARA also studied the physiology of these super-athletes. From studies of contemporary archers he calculated the amount of energy expended in 24 hours as about 8000 calories. He also computed the necessary initial velocity for the arrows to traverse the long veranda, which was only 5.2 meters high.

KIHARA was an active, public spirited, and influential citizen, strongly committed to conservation. In his later years he devoted a great deal of time to preservation of the landscape, a much-needed activity in that crowded and environmentally fragile country. He was especially active in preserving the native vegetation in the Hakone area not far from Mount Fuji. A particular concern was the increasing number of golf courses, which were interfering with the normal pattern of water runoff. As a botanist he was largely responsible for the Hakone Arboretum and edited a book of trees and other plants in this area (KIHARA 1971). He had a deep interest in a "living fossil" sequoia (*Metasequoia glyptoboides*) found in China and transplanted some trees to Japan. His favorite plant in the Hakone area was the dogwood (*Cornus kousa*), and he also transplanted American dogwood (*Cornus florida*) to the grounds of the National Institute of Genetics in Mishima.

KIHARA was far and away the best known Japanese geneticist in pre-molecular days. He was an honorary member of no less than 20 societies outside of Japan, including those in Russia, Britain, Sweden, Germany, and India. In the United States he was a foreign member of the National Academy of Sciences, the American Academy of Arts and Sciences, and the American Philosophical Society. I believe his nearest counterpart was N. I. VAVILOV. Both had great self-confidence, tremendous enthusiasm, and boundless energy. Their work was characterized, not so much by its brilliance and depth of insight as by its thoroughness and breadth, and by a willingness to try big things–large-scale experiments and long expeditions. And, most important, both had the ability to lead and inspire followers. Fortunately, in contrast to VAVILOV's tragically truncated career (CROW 1993), KIHARA lived a long life. He was intellectually vigorous until the end.

KIHARA liked to characterize himself figuratively as "a grain of wheat" and his photographic biography bears this title (KIHARA 1985). He had remembered the biblical parable of the sower whose seeds flourished and multiplied only when they fell on good ground.

Although I had met KIHARA on his trip to the United States in 1951, I first became well acquainted with him in 1957, when I had the good fortune to spend the summer at the National Institute of Genetics in Mishima working with MOTOO KIMURA. KIHARA was director at the time. I have vivid memories of his generous hospitality, his enthusiasm and physical energy on trips to see interesting plants and geological formations, his pleasure in leading foreign geneticists on a tour through a Sapporo brewery, and his delight in serving seedless watermelons to his guests. Wherever we went he seemed to know everybody and to be instantly recognized. He was Mishima's leading citizen, a role that I think he enjoyed. One anecdote will serve. Impelled by curiosity as to how the Japanese did such things, I went to a large public gathering at which Miss Mishima was to be chosen. And who turned out to be the judge to select the most personable and comely young woman? KIHARA, of course.

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