Nikolai Ivanovic Vavilov (1887-1943) [1]

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Nikolai Ivanovich Vavilov proposed theories of plant genetic diversity and participated in the political debate about genetics in Russia in the early twentieth century. Vavilov collected plant species around the world, building one of the first and most comprehensive seed banks, and he spent much of his life researching plant breeding and genetics. Vavilov also developed a theory of the historical centers of origin of cultivated plants. Vavilov spent most of his scientific career in Russia, although he studied abroad and traveled extensively. The ascent of geneticist Trofim Lysenko, favored by Joseph Stalin, and Vavilov's public criticism of Lysenko lead to Vavilov's arrest in 1940 and his death in prison three years later.

Vavilov was born in Moscow, Russia, on 25 November 1887 to Aleksandra Mikhailovna and Ivan Ilich Vavilov, a wealthy merchant. Vavilov had three younger siblings: his sister Alexandra, who became a doctor; his sister Lydia, who studied microbiology but died in 1913 due to smallpox; and his brother Sergei, who became a physicist and later president of the Soviet Academy of Sciences.

Vavilov began his undergraduate studies in 1908 at the Timiryazev Academy of Agriculture (formerly the Moscow Agricultural Institute) in Moscow, studying genetics and horticulture. Vavilov studied plant immunity and Charles Darwin [6]'s 1859 theory of evolution [7], and his undergraduate thesis was on slugs, titled, "*Golye slizni (ulitki), povrezhdayushchie polya i ogorody v Moskovskoy gubernii*" (Destructive Slugs of the Fields and Gardens of Moscow Province's). While some of Vavilov's professors at the Academy advocated for Jean-Baptiste Lamarck's early nineteenth century theory of evolution–that organisms could acquire traits in their lifetimes and pass them via heredity to their offspring–Vavilov supported Gregor Mendel's 1865 theory of heritability, and he supported Darwin's theory of evolution [7] through selection. The soil scientist Dmitri N. Pryanishnikov mentored Vavilov in his undergraduate studies and after his graduation in 1911, when he hired Vavilov as a researcher at the Academy from 1911 to 1912.

During this year as a researcher, Vavilov taught part-time at the Golitsyn Women's Agricultural School in Moscow. Vavilov worked with the Russian plant breeder Dionazas L. Rudzinsky from 1911 to 1917 at the Academy's agricultural experiment station in Moscow. In 1912 Vavilov moved to St. Petersburg, Russian, to study plant immunity under Robert Eduardovich Regel at the Bureau of Applied Botany and with Artur Arturovich Iachevskii at the Bureau of Mycology and Phytopathology. Vavilov married Yekaterina Nikolevna Sakharova, a colleague from the Academy, in 1912. Sakharova gave birth to a son, Oleg, in 1918.

Vavilov studied abroad in England from 1913 to 1914 for his master's degree research while enrolled at the Timiryazev Academy. He studied with the geneticists Rowland Harry Biffen, at Cambridge University [8], and William Bateson [9], at the John Innes Institute at Merton, London. Vavilov later credited Bateson as a great influence on his intellectual development. Vavilov studied wheat immunity to diseases, leading to his masters' thesis, which he completed in Russia due to the outbreak of World War I [10]. While in western Europe, Vavilov worked in Darwin's personal library, attended lectures by Reginald Punnett, visited the Vilmorin Institute in France, and met with evolutionary theorist Ernst Haeckel [11] in Jena, Germany.

Shortly after his return to Russia from Western Europe, Vavilov completed his graduate thesis, titled "Immunitet rasteny k infektsionnym zabolevaniam" (The Immunity of Plants to Infectious Diseases). Vavilov worked at the Academy until his first professorship. The Voronezh Agricultural Institute, in Voronezh, and Saratov University, in Saratov, jointly appointed him as a professor of genetics in 1917. Despite the ongoing Russian revolution in 1917, Vavilov remained immersed in his work.

In 1918 Vavilov published the book, *Immunitetrastenii k infektzionnyrn zabolevaniyam* (Plant Immunity to Infectious Disease). He proposed the *Zakon gomologicheskikh ryadov* (Law of Homologous Lines), which he presented in a lecture on 4 June 1920 at the Third All-Russian Congress of Selectionists held in Saratov, Russia. A corresponding paper, "The Law of Homologous Series in Variation," he published in English in 1922. Drawing on the theories of biologists like Charles Darwin [6], Hugo de Vries [12], and Gustav Heinrich Theodor Eimer, and using the methods of plant breeding and plant systematics, Vavilov explained in the papers how closely related plants tend to vary from each other, in similar patterns across species, for both genetics and morphology [13]. Vavilov illustrated his theory by showing how phenotypic traits follow parallel, predictable patterns in related crops such as wheat and rye. Later in his life, Vavilov would state that the theory applied more to phenotypic traits than to genes [14].

Around 1920 Vavilov began an affair with a former graduate student, Yelena Ivanovna Borulina, and separated from his first wife in 1926 to marry Borulina shortly thereafter. Borulina had a son with Vavilov, Yuri Nikolaevich, in 1928. Both of Vavilov's sons became physicists.

Vavilov's work in the early 1920s was supported by Vladimir Ilyich Lenin, the major Bolshevik political leader in Russia's post revolutionary socialist government. In 1923 Vavilov became a partial member of the Soviet Academy of Sciences, headquartered in Saint Petersburgh, then called Petrograd. In 1920, Vavilov's former mentor Regel died, and Vavilov replaced him as director of the Bureau of Applied Botany in Petrograd, and he began his work there in 1921. He led the department's restructuring into the All-Union Institute of Plant Industry in 1924, years later renamed the N. I. Vavilov Research Institute of Plant Industry (the VIR). The Bureau coordinated the collection, selection, adaptation, and use of diverse plant varieties for Russian agriculture, through plant breeding and comparative crop trials. By 1931 the Bureau's seed bank contained greater than 10 million varieties of seeds. In 1929 Vavilov coordinated the formation of the All-Union Lenin Academy of Agricultural Sciences, which housed the Bureau, and was elected a full member of the Academy of Sciences that year. At one point in the mid-1930s Vavilov managed greater than 20,000 government researchers. Vavilov directed the Bureau until 1940.

From 1908 to 1940, Vavilov traveled around the world and collected seeds, bringing back samples to the Soviet Union for characterization and storage. His first major exploration was in 1916 to Persia (later Iran) to collect local varieties of wheat, and in 1921 he went to the United States, where he met Thomas Hunt Morgan [15] and also bought seeds that would suit the agricultural conditions of the Soviet Union. He also collected seeds in Afghanistan in 1924. In 1926 he traveled the Mediterranean and Middle East; in 1929, East Asia; and from 1932 to 1933, Central and South America.

Vavilov developed his theory on the centers of origin of agricultural plants in a 1926 paper "*Tzentry proiskhozhdeniya kulturnykh rastenii*" (Centers of Origin of Cultivated Plants) and further elaborated it in monographs. He proposed that the areas with the most diversity of a plant variety and its wild relatives indicate where humans [16] first cultivated these plants. According to Vavilov, these areas of first cultivation represent the centers of evolutionary origin of some plant varieties. The center of origin of a particular variety of wheat, for example, would be the place where a diversity of genetic relatives–especially undomesticated weedy relatives–of that variety would exist. Unlike previous theories on this subject, Vavilov used traits like the number of chromosomes in the cells of organisms within a species to characterize and categorize genetic diversity within species.

Vavilov recognized five primary centers–southwestern Asia, southeastern Asia, the Mediterranean coast, South America, and Mexico–and several secondary centers or origin. He later revised his theory to seven primary centers of origin. Vavilov's *Centers of Origin of Cultivated Plants* influenced few until after World War II, when English versions of his maps were published. Since then, agricultural scholars around the world have studied his book and theories.

Vavilov's early research on plant immunity led him to theorize that plants and pathogens both evolved throughdifferentiation [17] and selection by environmental pressures. His work on plant immunity led to his later theories on the genetic diversity of crops, and on how such diversity contributed to disease immunity. In 1935 he published *Uchenie ob immunitete rasteny k infektsionnym zabolevaniam* (Theory of Immunity of Plants to Infections Diseases). In this work Vavilov proposed that as plants in different paces evolve immunities in response to local environmental pressures, he could use a plant's immunity to pathogens to infer the center of origin; that is, he could infer the location of their evolution [7] from their phenotypic traits, in this case their immune systems.

In 1927 Trofim Denisovich Lysenko, a public rival of Vavilov's, was recognized in the national newspaper for his skills in plant breeding. Vavilov followed Lysenko's work, but soon realized that Lysenko lacked a formal scientific education and was unaware of modern genetic concepts. Rather than testing by controlled experiment, Lysenko pursued his own methods of plant breeding, and in some cases manipulated his results. Lysenko promoted what scientists called vernalization, that is, exposing seeds to cold and moisture in order to change when they can be planted. He proposed vernalization as a solution to the problem of adapting crops to the cold northern climate of Russia. Lysenko argued that this technique would dramatically increase crop yields in Russia.

Further, Lysenko ideological commitments against modern genetics led to his belief in the evolutionary theories of Jean-Baptiste Lamarck, a biologist who had studied inheritance, in France in the nineteenth century. Joseph Stalin, another powerful member of the Bolshevik revolutionaries who became, after the death of Lenin, the major figure in Russian politics, also supported Lamarck's theory, so Lysenko gained governmental support. Vavilov did not, at first, publicly question Lysenko's techniques and instead encouraged Lysenko to work at the experiment stations that Vavilov managed, and to attend an international genetics conference with him. Vavilov said that he hoped that with some training, he could transform Lysenko from a promising, but unscientific, plant breeder, into an educated scientist. Lysenko declined Vavilov's offers.

Lysenko explicitly gained Stalin's support in the mid-1930s and his theories persisted in Russia through the late 1960s. Under Stalin's rule, the Soviet government wanted to see the immediate results of scientific agriculture. The process of plant breeding can take more than a decade to develop a new crop, but Lysenko's theories were seen as a quick fix to Russia's food shortages. Lysenko's vernalization techniques were used on a large scale after the state's takeover of farms in 1931.

Despite Vavilov's early ambivalence towards Lysenko's methods, the prospect of more productive Soviet agriculture encouraged him, and he promoted Lysenko's work internationally and nationally. Vavilov stated that vernalization was a useful technique for plant breeding, but that it should not be used to produce seeds for large-scale agriculture. Beginning around 1936, Lysenko openly criticized Vavilov and attacked him for his support of Mendelian genetics. As Lysenko gained political power, he increasingly challenged Vavilov's scientific enterprises. Vavilov, already under surveillance of the Soviet secret service, was considered suspect for his wealthy family and his ties to Western science. With the impending trouble of Lysenko's political influence as early as the 1930s, Vavliov had lobbied for the diplomatic protection of his colleagues when some of them were arrested. By 1937 Vavilov's memoirs and correspondences show that he began to fear for his future under Stalin's rule and Lysenko's influence. Several of his colleagues had already been arrested and killed.

By 1938 Lysenko had replaced Vavilov as president of the All-Union Lenin Academy of Agricultural Sciences, the highest post in Soviet agricultural science, although Vavilov remained employed in his other positions. Vavilov defended his theories against Lysenko's attacks, however, Vavilov's support of and ties with Western science clashed with Stalin and Lysenko's Marxist science, which rejected contemporary genetics while still adopting theories of evolution [7]. Vavilov also suffered when Hermann Muller, an US geneticist and socialist that he had recruited to work in Moscow, publically linked Lamarckism [18] to eugenics [19], a topic banned by Stalin. Muller later fled to western Europe.

Vavilov was elected chairman of the International Congress of Genetics in 1939, after which he unsuccessfully attempted to hold the Congress in Moscow. In 1939 Stalin questioned Vavilov about how to raise crop yields. According to some historians, Stalin had plans to arrest Vavilov but did not want to attract international attention; the outbreak of World War II provided some cover.

Vavilov was arrested in 1940 while on a scientific expedition to Ukraine. He was formally accused of being a traitor and a British spy, and he was sentenced to death, a sentence later commuted to a twenty-year term in a work camp. Vavilov was transferred from a prison in Moscow to a prison in Saratov in 1941. While imprisoned, in 1942 Vavilov was inducted into the Royal Society of London as a foreign member. Vavilov remained in prison in Saratov until he died from starvation on 26 January 1943.

One of Vavilov's most cited works is a posthumous publication, *The Origin, Variation, Immunity and Breeding of Cultivated Plants*, published in English in 1951. In this work Vavilov argued that diversity of plant varieties was not evenly distributed throughout the world, and that the centers of origin of a species contained the most genetic diversity related to the original variety. Vavilov noted that mountainous regions were especially rich in plant diversity. In terms of immunity, Vavilov said that the same species of plants could exhibit very different immunities in Western versus Eastern parts of the world. Much of this book was devoted to current practices in wheat breeding, including Vavilov's discussion of chromosomal grouping in different wheat varieties. Another posthumous collection of his works was published in Russian in 1987 and English in 1992 as *Origin and Geography of Cultivated Plants*. This work collects Vavilov's speeches and papers from 1926 to 1940 with his monograph, *Centers of Origin of Cultivated Plants*. The Russian government, for his contributions to genetics, later recognized Vavilov's scientific contributions.

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