From spring & winter wheat to the Lamarckist transmutation theory, to the tragedies of Lysenkoism in Soviet Russia, to the elusive florigen and plant natural variation & epigenetics research: Here's...

A Short History of Vernalization

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Humans have known for centuries that some plants would only flower and produce yield in late spring or summer if they are planted and germinated before winter[1]. Such crop plants display an enhanced cold tolerance, and survive through winter with the help of a protective layer of snow, sheltering them from freezing[1]. The benefit of growing such winter varieties is that they produce higher yield than spring varieties[1]. Importantly, such winter varieties don't just tolerate winter weather – they actually require it, as they won't flower at all without this period of cold[1]. Today, this cold treatment is designated '*vernalization*'.

Spring vs. Winter Wheat – Different Plants or Different Environments? (1800s)

Around the year **1800** it was still a matter of debate what caused the difference in behavior between spring and winter varieties of the same crop[1,2]. According to John Lawrence, a farmer and author of the 1800 '*New Farmer's Calendar*', '*it has been disputed, whether any specific difference exists between spring and winter wheat*'[2]. The question at the time was, if these are actually different plants, or if their behavior was simply modified by their environment[2]. The latter would mean that it should be possible to 'train' them to behave differently and adjust to a new environment[1]. This was not so much an issue for farmers in Europe and Asia, where wheat varieties had been grown for centuries and were bred to be optimized for the local conditions[1,3]. But the situation was different in the USA[1,3]. Here, wheat plants were imported from Europe, and some of the varieties that performed well in their respective countries of origin, failed to do so when sown in the US[1,3]. Especially in the harsher climates of the northern states, this became a major issue[1,3]. In the fertile Genesee Valley in Flint, Michigan, for example, farmers failed to establish any of the most productive imported European and Asian varieties, as they died off during the harsh winters[1,3]. It was only in the **1820s**, that a variety then known as Genesee Flint Wheat was established as a successful variety[1,3]. In this context, studying winter wheat suddenly became an important issue, as plants that could survive under specific local conditions were urgently needed[1]. In **1860**, agriculturist John Hancock Klippart published his, at the time definitive book on '*The Wheat Plant*', describing all the results and observations made by US farmers and agriculturists over the past decades, when experimenting with different plants and conditions[1]. When it comes to winter and spring wheat, he also touches on the controversial topic of conversion[1]. Here, he describes that winter wheat could be transformed into spring wheat, and vice versa, through a multi-generational adaptation process; one of the many attempts that desperate farmers used to optimize their plants to the local environment[1]. He describes how few of the winter wheat plants will actually flower and ripen in the same year if they are brought out in spring, and that they would be very weak and only yield moderate crop[1]. If, however, those seeds will be sown again in the following season, they would already grow much better, and eventually, over several seasons, reach a productivity level equal to spring wheat[1]. Similarly, if spring wheat is sown out before winter, and if some plants would survive the cold and frost, then the seeds of such plants will produce plants that will perform much better in the following season[1]. Another conversion experiment was conducted in **1837/38** by Colonel Abbott, who reported his findings in *The Monthly Genesee Farmer*[4]. Abbott used Flint winter wheat, which he soaked in a tub of water until sprouting[4]. At that point, he placed the seedlings into a box, which he exposed to cold[4]. Eventually he sowed these seedlings out in April and May, as one would do with spring wheat[4]. Those seedlings grew to full plants, giving seed just as spring wheat would[4]. This experiment may therefore be the first documented vernalization experiment[4]. While Klippart is generally supportive of these *conversion* experiments, he is very critical of the so-called *transmutation* theory[1].

The transmutation theory describes a metamorphosis-like process, turning one plant into a completely different one[1]. A famous such '*pseudo-observation*', as Klippart calls it, was the transmutation of wheat into *Bromus secalinus* ('chess' or 'cheat'), a rye-like weed[1]. According to supporters of the theory, the transmutation can be caused by either (I) excessive moisture and cold in the spring months, (II) pasturing in the spring, or (III) hauling a wagon over the field, transmutating every seed that gets squashed by the wheel[1]. The prevalence of this belief in the **1840s** eventually led Benjamin Hodge, an agriculturist and respected nursery owner from Buffalo, New York, to offer a 100$ reward to anybody, who could prove that wheat was indeed transmutated into chess[1]. For this, he worked with the New York State Agricultural Society, who appointed a supervisory committee to evaluate the outcome of the challenge[1]. The 100$ prize was claimed by one Samuel David, who performed the following experiment: He thoroughly cleaned wheat seeds to get rid of all chess contaminations[1]. He then germinated them in a pan, where he also subjected them to all possible harsh treatments that would supposedly lead to transmutation (it is not documented if he wheeled a wagon over the pan though)[1]. He then sowed those seeds into regular soil, from where eventually not just wheat, but also chess heads came up[1]. Those seedlings were then presented to the commission, showing some cases where the chess stalk seemed to indeed be emerging from a wheat seed[1]. However, careful microscopic investigation of the seedlings eventually demonstrated that these stalks merely grew through or along the rotting wheat seeds, and '*the examination therefore did not prove anything in favor of transmutation, and as there were many possible ways in which the chess might have been scattered on the soil, the whole experiment was admitted by all parties to be inconclusive*'[1]. '*From hasty observations, equally hasty inferences are generally made, and false conclusions are the result*', Klippart concludes[1].

There can be little doubt that the supporters of both, the conversion and the transmutation theories, were heavily influenced by Jean Baptiste Lamarck's **1809** book '*Philosophie Zoologique*', which describes Lamarck's evolutionary ideas for the origin of species[5]. Those ideas form the basis for Lamarckism – the dominant evolutionary theory at the time, prior to the publication of Darwin's '*On the origin of species by means of natural selection (...)*' in **1859**[5,6]. '*Transmutation*', according to Lamarckism, describes the evolution of complex organisms from simple ones through the acquisition of required traits[5]. Basically, new traits will evolve when they are needed, while existing traits may be lost if they are not actively being used[5]. Once acquired, traits then become heritable through the generations, the transmutation is complete[5]. Interestingly, the word '*transmutation*' was actually coined in **1766** by German botanist Joseph Gottlieb Kölreuter, a pioneer in the field of plant sexual reproduction and hybridization, who used the word to describe new breeds of plants that he created via hybridization[7].

Not surprisingly, no actual transmutations were ever reported in the following years, and the transmutation theory was eventually abandoned. However, it did experience a revival in an especially perfidious form in Soviet Russia, in the early 20th century, which will be discussed here later. Actual research into the cold tolerance and cold requirements of different crop varieties only seriously started after Klippart had published his book on the wheat plant in 1860.

Cold Requirement Studies and Photoperiodism (1900 – 1927)

The 20th century brought the first major scientific publication describing experiments with different crop plant varieties to study their individual cold requirements[8]. In **1910**, German botanist Gustav Gassner was given access to three large refrigerators at the Seed Research Institute in Hamburg, Germany (Hamburgisches Botanisches Saateninstitut), with constant temperatures at 1-2°C, 5-6°C or 12°C, a luxury at the time[8]. Using these refrigerators he systematically tested plants for their response to these three different temperatures, length of exposure to these temperatures and the developmental state during which the cold treatment was applied[8]. He found that different plants do indeed require different temperatures to induce flowering, that the temperature required can be linked to the developmental age of the plant (i.e. older plants require colder or longer cold treatments), and that it doesn't need to be the plant that is treated, but it can suffice to treat imbibed seeds[8]. Furthermore, he also discusses that it is not just the temperature, but also other environmental factors that play a role[8]. These factors include sugar content and, more importantly, light conditions – a very important point still mostly overlooked at the time when studying flower induction[8]. Additionally, Gassner even discussed a certain rhythmic pattern that plants seem to follow in their growth throughout the year, thereby coming very close to describing photoperiodism[8]. He published his extensive studies in a **1918** book, which triggered a boom in vernalization research for the following decades[8,9]. In fact, by the early **1930**s, the field was so well funded, that Gassner's colleague Prof. August Seybold disparagingly labelled it '*Modeforschung*' (i.e. 'trendy research')[9]. Gassner himself, however, could not benefit from this new trend[9]. Being an outspoken opponent of the rising German Nazi-party and Adolf Hitler, he prohibited the Hitler salute and any political activities in his institute, resulting in his removal from the institute, imprisonment, and eventually his exile to Turkey in **1934**[9]. It was only in **1945**, following the end of the Second World War, that he was again appointed as Rector and Professor at his old Institute of Technology in Braunschweig, Germany[9].

While Gassner already touched on the interconnectedness between cold treatment and day length, it were Wightman W. Garner and Harry A. Allard who did the first extensive analysis on the effect of day length on flowering time[10]. They exposed several plants to different day length regimes and light intensities, and comprehensively described their individual light requirements[10]. Regarding day length they confirmed that plants will only flower and set seed if day length reaches certain limits, and that day length and cold temperatures are interrelated to induce flowering[10,11]. However, depending on the plant, long or short days could be favorable for flowering. '*The term photoperiod is suggested to designate the favorable length of day for each organism, and photoperiodism is suggested to designate the response of organism to the relative length of day and night*', they conclude in their work[10]. In their follow up studies they even tried to 'localize' the response to day length within the plant[11,12]. They previously showed that *Cosmos bipinnatus* (Mexican aster) would not flower under continuous light, but quickly under short day conditions[11,12]. So to test if this is a local, or general response, they exposed different branches of the same *Cosmos* plant to different day lengths[11,12.] And indeed, they were able to show that the branch exposed to winter day light conditions quickly flowered, while the continuous light branch continued to grow vegetatively[11,12].

While this early research into cold and light requirements of plants was pursued primarily in Europe and to some extent also in the USA, agricultural research, and specifically work on the cold requirement of winter varieties, took a very different turn in Soviet Russia at the start of the 20th century.

The Russians (Michurin, Vavilov & Lysenko) and Jarovization (1890 – 1930)

Towards the end of the **19th century**, Ivan Vladimirovich Michurin, a railway worker from central Russia, rose to become one of the most important figures in Russian agriculture[13]. Michurin had cultivated fruit trees all his life in his parent's garden, and over the years this hobby gradually developed into something bigger[13]. Despite his family being relatively poor, Michurin spent all of his money on seeds and books about gardening and plant cultivation[13]. His job with the railway enabled him to travel to all the famous gardens in central Russia, where he studied the 'state of gardening' in his home country'[13]. Eventually, in the **1880s**, he noted that '*after 15 years of comprehensive theoretical and practical studies of plant life and, mainly, gardening and its needs in Middle Russia ... I have concluded that the level of our gardening is too low*'[13]. He therefore took it onto himself to change this, founding a fruit tree nursery in **1888**[13]. Over the course of the next five decades Michurin's nursery produced over 130 new varieties of fruit, such as apples, pears, cherries or plums[13]. He utilized a breeding method based on distant hybridization, where he cross-pollinated distantly related plants in order to produce new varieties[13]. For this, he developed several new techniques, including methods to overcome incompatibility and even a primitive form of electroporation and cytogenetics[13]. He also worked out novel selection processes to speed up this part of the work[13]. Michurin published his studies in Russian horticulture journals and by the early **20th century** he had authored around 100 scientific papers[13]. During this time, he tried to connect with the Russian Department of Agriculture in order to receive funding for his research[13]. The Department however, failed to see the value of Michurins work and merely offered him smaller grants if he would conduct some experiments for them under their strict control, which Michurin rejected[13]. However, while the Russian government did not realize the value of Michurin's endeavors, they made sure that he did not strike a deal with the American government either, which would have been happy to relocate him, his family and the entire nursery to the US[13]. Michurin recalled later: '*higher spheres had prohibited me leaving for America...*'[13]. He finally did get the recognition he deserved in 1920, following the Soviet revolution, and with the help of Vladimir Lenin and another agronomist, Nikolai Vavilov[13].

In the early **1900s** Nikolai Vavilov was the most important agronomist in the Soviet Union and the Lenin-appointed director of the Lenin All-Union Academy of Agricultural Sciences[14]. This basically put him in a position where he was responsible for the entire sector of agricultural research in the Soviet Union[14,15]. Vavilov was considered a pioneer not just in Soviet Russia[14,15]. Following his graduation from Moscow Commercial College in **1910**, he entered the Moscow Agricultural Institute from where he received his PhD for his work on the use of Mendelian genetics for the targeted breeding of more efficient crops[15]. He then joined William Bateson at the John Innes Institute in the U.K., where he studied the resistance and susceptibility of different wheat accessions from all over the world to fungal pathogens[15,16]. For this work he could apply his interest in studying the genetic diversity of the world's crop plants to improve crop plant performance – a research program far ahead of its time[15,16]. He then continued his work as a lecturer and professor at the Saratov Agricultural Institute in Russia until **1921**, when Vladimir Lenin personally appointed him as head of the Applied Botany, and eventually director of the Lenin All-Union Academy of Agricultural Sciences[15]. In this position, Vavilov emerged as one of the most important plant biologists of the 20th century. In **1922** he published the influential law of homologous series in variation and genetic mutability[17]. According to this, Vavilov argued, plant breeders should not try to randomly breed better crop varieties, but look for beneficial phenotypic traits in closely related plants (based on Carl Linneaus' work[18]), and then breed specifically for this trait – an educated guess approach[15,17]. He later added that homologous genes (based on Mendel's work[19]), could be the basis for the observed phenotypic similarities[17]. Again, his work was way ahead of its time. Knowing about the importance of genetic variability within plant species, Vavilov then personally undertook or directed several expeditions to all parts of the world to collect different natural accessions of the most important crop plants[15,20,21]. He analyzed these plants for their genetic and phenotypic diversity across the habitats from where they were collected, arguing that the origin of a plant (i.e. the geographical region where domestication started), would be the region of its highest diversity[20,21]. Based on this theory, he defined several '*centers of origin*', such as the Middle East for different wheat, barley and rye varieties, eastern Asia as the center of origin for soybean, rice or sorghum, and Central America for maize and potato[20]. He further extended and refined this monumental and groundbreaking work between **1925** and **1933**[20,22]. Moreover, he maintained and catalogued all the seeds he collected on his travels around the world, creating the largest seed collection for decades, with over 250.000 samples, representing the world's diversity of food crops[14]. The importance of this collection was re-confirmed when it was incorporated into the Svalbard Global Seed Vault between **2005** and **2011**[23,24]. And finally, in his role as director of the Lenin All-Union Academy of Agricultural Sciences, Vavilov was also an outstanding organizer. While in this position, he opened over 400 research stations and institutes throughout the Soviet Union, thereby establishing the Soviet Union as a world leader when it came to agricultural research, genetics and plant breeding[14].

Following the **1917** October Revolution in Russia, the new Soviet Government immediately seized all agricultural businesses, claiming them as national assets[13,25]. Michurin's nursery was no exception to this[13]. However, Michurin, a supporter of the Soviets, was able to strike a deal with the local land department, which recognized the value of Michurin's work, therefore allowing him to keep supervision of his nursery[13]. The district commissariat of agriculture furthermore relayed the importance of Michurin's work to The People's Commissariat of Agriculture, eventually garnering him the governmental recognition he deserved[13]. After that, Vladimir Lenin personally promoted Michurin's work publicly, further elevating his status[13]. By **1920**, Vavilov was also aware of Michurin's work and proposed to assemble a scientific inventory of his nursery's gene pool[13]. However, shortly after the Soviet's seized power, the Russian agricultural sector faced severe problems[13,25]. Between **1925** and **1928**, harsh winters with little or no snow had killed off the winter crops, resulting in severe yield losses and famine[13,25]. Stalin's forced collectivization of agricultural farms resulted in inefficient and mismanaged kolkhozes that dramatically decreased productivity[13,25]. And on top of that, Stalin's purges resulted in the murder of some of the most productive farmers due to their relative wealth, further decreasing agricultural production and, equally important, causing the loss of crop varieties due to the subsequent mismanagement of the farms by Bolshevik officials[13,25]. Accordingly, one main objective for the agricultural scientists during that time period became the breeding of new, better performing varieties of food crops[26,27]. For this, Vavilov decided on Michurin-inspired distant hybridization experiments, to breed better performing cereal grain varieties[28]. But one major problem that he encountered with these experiments was the need to synchronize the different plants so that they would flower simultaneously and could be cross-pollinated[28]. At this point, the work of another young scientist came to his attention[28].

Trofim Denisovich Lysenko was an agronomist, who in **1925** started to work on soil enrichment at the Experimental Agricultural Station in Ganja, Azerbaijan[28]. In the face of the sustained famine in the country, however, he switched his focus to the conversion of winter into spring wheat, to avoid the harsh winters[26]. In his experiments, he basically repeated the experiments that Colonel Abbott described in 1837: He soaked seeds in water and chilled them at low temperatures for several weeks, before sowing them in late winter or spring[28,29]. As was the case for Col. Abbott, those seeds then germinated in spring and flowered in the summer[28,29]. In his **1928** publication describing these results Lysenko named this process of cold treatment 'jarovization' (from jarovoe, the Russian name for spring cereals)[28,29]. These experiments came to the attention of Nikolai Vavilov, who figured that Lysenko's jarovization could be a useful tool for him to synchronize the flowering of his distantly related crops[28]. He therefore invited Lysenko to speak at the **1929** national conference of agricultural science in Leningrad, despite the fact that Vavilov's main expert in the field of plant physiology, Nikolai Maksimov, was very critical of Lysenko due to his strong ego and inability to take advice from colleagues[28]. While Vavilov was only interested in jarovization as a tool to synchronize flowering, Lysenko had much grander aims[28]. At the conference, he tried to sell jarovization as a tool to permanently transform winter wheat into spring wheat[28,30]. Despite this, Lysenko's presentation did not receive too much attention at the conference, which didn't sit well with the ambitious scientist[30]. In order to prove the importance and applicability of his discovery, he planned a big publicity stunt[28]. Together with his peasant father, he jarovized lots of winter wheat seeds and sowed them out in spring[28]. In summer, the family's field was full of winter wheat, ready to be harvested[28]. For the rural community, this was close to a miracle, and accordingly this demonstration found widespread coverage in local and national newspapers[28]. On the back of this success, Lysenko became known in Russia as a sort of miracle worker/scientist, and actually obtained his own research laboratory at the Ukrainian Institute for Genetics in Odessa[28]. There, he soon found that mass jarovization of winter wheat was simply not practical to actually obtain a significant increase in agricultural productivity, and he therefore switched his attention to jarovizing spring wheat, arguing that it would ripen faster and produce more yield[28]. But again, his claims of a significant yield increase could not be confirmed in any scientific tests[28,30].

However, despite these failures and an increasing number of critical voices among the Russian agronomic community, Lysenko was still regarded highly, not in the least because of Vavilov's support and his reputation for practical achievements in the public eye, based on his well-documented field trial[28,30].

Vernalization, Lysenkoism, and the 1948 Meeting of the Lenin All-Union Academy (1931 – 1965)

By **1931**, the situation in Russian agriculture had worsened even more[28,30]. And now, the government also started to directly interfere with academic research[30]. Increasing pressure from the Stalinist government to include Marxist ideology in the sciences, meant that the field of genetics came under fire[30]. Idealistically, Stalin's interpretation of nature was based on Marxist-Leninist dialectical materialism[27,31,32]. As such, nature had to be seen as a unified whole, constantly developing according to guiding environmental pressures[27,31,32]. Accordingly, anything could be developed into any direction, if the correct pressure was applied by shaping the appropriate environment[27,31]. On a society level this means that a classless society could be created if the right pressure was applied from above, and on an individual level, that the Soviet government could (and should!) actively form its citizens and their attitudes to become good Marxists and communists by creating the right environment (i.e. the right pressure from above) [27,31]. Evolutionary wise, this ideology borrows from Lamarckism, in that new traits in an organism will constantly develop in order to resolve existing constraints (pressures), and traits acquired this way would furthermore be inherited as a 'state' of an organism[27,31]. Thus, this ideology was to be adopted by the sciences as well[25]. As a plant-specific example: According to Lysenko, winter wheat, once jarovized, would remain jarovized for the coming generations, having been pressured into becoming spring wheat[14,25]. Lysenko's work therefore fit very well into this ideology[27,31]. Lysenko even went as far as claiming that continuously plucking a leaf from a cotton plant, would eventually result in leafless offspring[25]. However, genetics and Darwinian evolution were considered inconsistent with this Marxist-Leninist version of dialectical materialism[31]. Under this situation of famine, starvation and increasing pressure to adhere to Soviet ideology, the Communist party issued a **1931** decree that ordered agricultural researchers to create new and more efficient crop varieties within the next 4-5 years[26]. While the leading scientists protested this unrealistic aim, Lysenko jumped at the chance to establish himself as a leader, and claimed that using his jarovization technique, he would be able to breed such new varieties within just two years[26]. This promise, Lysenko's public reputation as a miracle worker, and his publicly demonstrated willingness to bend the science to fit Marxist ideology, made him Stalin's personal favorite, which would eventually result in the complete devastation of Soviet agricultural sciences[26].

During this time, Lysenko and his jarovization also received some international recognition, and in **1933**, the British Imperial Bureau of Plant Genetics published a bulletin focused on Lysenko's work[33]. In this bulletin, the latinized version of jarovization, '*vernalization*' (from 'vernum', latin for spring), is first used[33,34]. But by **1935**, Lysenko had nothing positive to present[21,31]. He was not able to produce any new varieties, and all his work using jarovization proved 'ineffective', as the 'successes' he reported were all based on falsified data and accordingly were not reproducible by independent scientists[21,31]. Lysenko reacted to these failures with anger, claiming that his work and progress have been undermined by the other leading scientists, explicitly naming Vavilov and their support of modern genetics[21,31]. This conflict between the two philosophies came to a head at the next congress of the Lenin Academy of Agricultural Sciences in Moscow, in **1936**[21,31]. Lysenko and his followers spoke in support of Marxist-Leninist Dialectical Materialism, and heckled the other scientists, who did their best to defend modern genetics and agricultural practices[21,31]. Vavilov himself gave two speeches during the Congress defending the application of Mendelian genetics and Darwinian evolution, but eventually it became clear that Lysenko had the backing of Stalin, and thus, the issue had already been decided[21,31]. Vavilov lost his position as the Head of the All-Union Academy of Agricultural Sciences, and in the following years several up-to-then unknown authors published papers claiming that all of Vavilov's works were fraudulent, including his work on the '*centers of origin*' and '*The Law of Homologous Series in Hereditary Variability*'[21]. Genetics, even the concept of the gene, Mendelian inheritance and Darwinian evolution were subsequently considered reactionary and idealistic, even though they were only formally outlawed in 1948. Lysenkoism took their place, despite Lysenko preferring to call it 'Michurinist agrobiology'[27]. Lysenkoism was based on Lamarckism and the transmutation theory, but specifically adds that crops can also be 'trained' through environmental pressure to behave in a certain manner[27,35]. This included not just the transmutation of winter into spring wheat, but even the transmutation of wheat into rye or barley[35]. Trying to capitalize on Michurins name and reputation, Lysenko claimed that Michurin also bred his plants employing such a 'training' approach in line with party ideology[26]. Conveniently, Michurin had passed away in 1935, and was not able to defend himself against this cooption[26].

In the following years, Lysenko continued to be criticized by his fellow Soviet scientists, while Vavilov, despite being removed from his positions in the Academy, remained a highly respected proponent of modern genetics[14]. As such, Lysenko realized that Vavilov would always be a problem to his authority[14]. In **1940**, following a heated dispute between Vavilov and Lysenko, Vavilov was arrested by agents of the People's Commissariat for Internal Affairs. He was presented with charges of being a right-wing conspirer and spy for the British Empire, and quickly convicted and sentenced to death[14]. While this sentence was eventually commuted to 20 years of imprisonment, Vavilov died on January 26th, **1943**, of cardiovascular failure and dystrophy, caused by starvation and sickness after several months in solitary confinement[14]. '*We shall go to the pyre, we shall burn, but we shall not retreat from our convictions*', he had prophesized in 1939. Subsequently, the government imposed a *damnatio memoriae* on Vavilov, attempting to erase him from history[14].

For Lysenko, things only got slightly better following Vavilov's removal. Criticism of Lysenko, by then referred to as a 'Dictator of Biology', continued to mount in the absence of any presentable results[26,27]. By the time the important Meeting of the Lenin All-Union Academy of Agricultural Sciences came closer in **1948**, Lysenko was forced to act. In the lead-up to the meeting, Lysenko sent a letter to Stalin where he reassured himself of the support from the Dictator[26,27]. Simultaneously, he promised to produce a new wheat variety in the coming year that would increase the countries wheat production tenfold[26,27]. Together, the two 'dictators' then carefully crafted and edited Lysenko's speech for the meeting, which aimed to once and for all silence the critics[26,27]. Lysenko's speech, entitled '*The Situation in Biological Science*', then took up the complete first day of the meeting[26,27,36]. In it, Lysenko spoke in favor of his Michurinist agrobiology, while speaking of modern genetics as reactionary pseudoscience and a bourgeois perversion[26,27,36]. As a consequence, the Politburo officially prohibited the disciplines of modern genetics and Darwinian evolution, drafted a list of laboratories that were to be shut down, and a list of scientists that were to be removed[26,27]. Overall, '*127 teachers, including 66 professors, were dismissed (...) the total number of those (...) dismissed, demoted, or removed (...) amounted to several thousand*'[27]. With this purge, Lysenko had finally rid himself of all critics, and biological science was now completely replaced with Lysenkoism[37]. However, by the time of Stalin's death in **1953**, Lysenkoism had still not produced any real useful results[37]. But since Lysenko had installed loyal followers on virtually every important scientific position, no criticism was ever voiced publicly[37]. Stalin's successor, Nikita Khrushchev, was similarly impressed by Lysenko as was his predecessor, and he therefore remained in office[38].

While Soviet Russian plant science was totally under tight control by Lysenko, researchers in other Soviet satellite states, such as Hungary and, even more so, Eastern Germany, still enjoyed a certain amount of freedom in their work[39,40]. The position of Eastern Germany was unique in the sense that Berlin was not yet separated by the wall, which was first constructed in 1961[40]. Accordingly, if the Eastern German regime would have pressed the doctrine of Lysenkoism onto its scientists too aggressively, they could simply have crossed the open border into Western Germany (though the role of Hans Stubbe and others in the active resistance against Lysenkoism must be mentioned as well)[40]. In Hungary, in **1953**, György P. Rédei, a young and talented plant biologist, was ordered by the Ministry of Agriculture to confirm Lysenko's results[39,41]. Specifically, he was asked to confirm the finding that winter wheat could be transformed into spring wheat by vernalization, and that the vernalization state would then be inherited in the future generations[39,41]. Notably, he was not assigned to 'test' Lysenko's claims, but explicitly to 'confirm' them[39]. Not surprisingly, Rédei could not substantiate Lysenko's results, and being a scientist of high integrity, he also published his own results accordingly[39,41]. Rédei's paper, published in Hungarian, was subsequently translated into Russian and republished in the Russian journal Izvestiya Akademii Nauk SSSR[39]. However, when Rédei requested a back-translation into Hungarian, he found that the journal's editor, Ivan E. Glushchenko, had altered his results so as to confirm Lysenko's work[39]. While Rédei was reportedly unhappy about this, this act may well have saved him from punishment from the Hungarian Stalinist Rákosi Government[39]. Only three years later, in November **1956**, when Soviet tanks rolled into Budapest to violently squash a student uprising against the communist dictatorship, Rédei and many of his fellow scientists eventually fled the country and thereby freed themselves from the shackles and constant threat of Lysenkoism[39]. Taking with him a vial of *Arabidopsis thaliana* seeds he had just received from Friedrich Laibach, Rédei became a temporary Assistant Professor for plant biology at the University of Missouri, USA, where his work resulted not just in the establishment of the Landsberg *erecta* and Columbia-0 *A. thaliana* lines, but also made him the 'Godfather of *Arabidopsis* research' in the process (see also 'A Short History of *Arabidopsis thaliana (L.) Heynh.* Columbia-0')[39,42].

Back in the Soviet Union, Lysenko's critics got louder once again in **1956**, when news of the success of hybrid corn in the USA made it to Russia[35]. In 1908, George Shull had described his observation of hybrid vigor in a corn field, the fact that hybrids between two inbred lines would appear more uniform and produce a higher yield than selfing within a single line would[43,44]. Research in the following years resulted in a rapid switch towards this approach to create hybrid corn by farmers in the US[45]. Lysenko however, disapproved of hybrid corn as he considered it part of modern genetics[35,45]. By the early 1950s almost all corn in the US was hybrid, and the astonishing success made it obvious to the Russians that they were missing out on a valuable discovery[35,45]. This time, the resulting backlash Lysenko received for his decision to ban hybrid corn was so strong that it actually forced him to resign as president of the Academy of Agriculture[35]. In the following years, Lysenko once again regained control of the Academy of Agriculture with Khrushchev's help, but his authority was irreversibly weakened following this revolt[35]. Criticism again reached a boiling point in **1962**, when three of the most prominent Soviet physicists, Yakov Borisovich Zel'dovich, Vitaly Ginzburg, and Pyotr Kapitsa, presented a case against Lysenko, explicitly proclaiming his work as pseudoscience[27,35,46]. Following Khrushchev's dismissal as the First Secretary of the Communist Party in **1964**, the president of the Academy of Sciences officially declared that Lysenko's immunity to criticism was voided, and in **1965** he was finally removed from his post for good[35].

While this episode in Russian history is now generally seen as a prime example of what can happen when ideology is forced upon science, there are unfortunately still some revisionists who try to paint Lysenko as an honest researcher who discovered vernalization and, in some instances, laid the foundation for plant epigenetics[31]. These are a minority, however, and the majority of people see Lysenko as the pseudo-scientist that he was[31].

Florigen, Vernalization in *Arabidopsis* & Formal Definition (1936 - 1965)

Curiously, one major breakthrough in understanding the mechanisms underlying the control of flowering in plants was actually achieved in Soviet Russia during those troubled times[47]. Mikhail Khristoforovich Chailakhyan, a PhD-student in Moscow in the 1930s, was studying photoperception in *Chrysanthemum*[47]. He found that under short-day conditions *Chrysanthemum* plants flower quicker than under long-day conditions, and then went on to demonstrate that it was sufficient to expose the leaves to a certain light regime in order to induce flowering[48]. Therefore, it appeared to be possible to uncouple the locations of photoperception (leaves) and response (inflorescence)[48]. He then conducted subsequent experiments, such as grafting the main stem of a long-day flowering plant onto the rosette leaves of a short-day flowering plant, demonstrating that the long-day flowering stem would now produce flowers under short-day conditions[47,48]. These experiments led him to propose that a substance produced in the leaves must exist, which then moves into the inflorescence where it induces flowering[47,48]. Believing that this substance might be a plant hormone, he named it florigen ('blossom-former') in **1936**[47,48]. As there was only one plant hormone definitely described at the time - Fritz Kögl described and named auxin (greek for '*to grow*') in 1931 - Chailakhyan's finding promised to be a major breakthrough[47–49]. At the same time, it is important to note that Julius Sachs already speculated in 1880 that a mobile leaf-produced substance might be required to induce flowering, based on his earlier findings since 1863[50,51]. Chailakhyan presented his work as part of his thesis defense in **1938**, with Lysenko being part of the committee[52]. Upon hearing this hormonal theory of plant development, Lysenko went into a rage and attacked Chailakhyan's theory in '*broken, brief, and harsh phrases often unconnected with each other*', as Chailakhyan remembered in 1988[52]. Plant development guided by internal hormones was incompatible with Lysenkoism, claiming that plant development is guided by the environment and external forces[52]. Chailakhyan was denied his PhD, and in the following years was continually harassed and demoted from his academic positions numerous times[53]. But, while his supervisor Prof. Richter was dismissed from the institute, Chailakhyan was able to stay and continue his research in low paying positions, thanks to the help of several supporters who repeatedly rehired him every time he was fired[53]. Among those supporters was also Nikolai Vavilov, who had taken note of Chailakhyan's talent and suggested to Lysenko that Chailakhyan could re-submit an edited version of his thesis, that might appease both sides[53]. This proposal was rejected by Lysenko[53]. Chailakhyan managed to stay in research until the end of Lysenkoism though, and finally picked up his work on flowering time, trying to identify the substance that was his theorized florigen[53]. He eventually became one of the most famous Russian plant biologists, and a highly respected member of the plant science community worldwide – staying active in research until his death in 1991[53]. Unfortunately, without the tools of modern molecular biology and biochemistry, he was never able to identify florigen[53].

While all of this was going on in Soviet Russia, vernalization research in Germany did not stop with the work of Gustav Gassner. Chailakhyan's work on florigen got German botanist Friedrich Laibach interested in solving the mystery of what makes a plant flower[54]. Or, in his own words *(translated by me)*, taken from the opening paragraph of his **1940** paper: '*If one finds the plants in the rooms or on the balcony of a house to be in especially nice bloom, one tends to compliment the housewife: 'you seem to have the right touch'. – therein lies the confession though, that one does not really know what treatment is necessary to achieve this blooming.*'[54]. At the time, Laibach was already lobbying for the adoption of *Arabidopsis thaliana* as a plant model organism and had built a collection of natural accessions that he and his colleagues had collected all over Europe on their travels (see also 'A short history of

Arabidopsis thaliana (L.) Heynh. Columbia-0'[42])[55]. He now intended to use this collection to analyze the flowering time of these accessions in response to different day lengths (he grew them in a warm greenhouse as he did not take temperature into account yet)[54]. He found that all accessions flowered at one point, but that the flowering time varied dramatically; between 12 days post germination or only after the second year post sowing[54]. He furthermore found that the accessions from similar geographical regions also behaved similarly, specifically, he found that the accessions from regions around the Mediterranean Sea seemed to require less hours in light, while further north they required longer days, and the Scandinavian accessions turned out to be biannual[54]. He included the effect of temperature in his follow-up work in **1951**[56]. Here, he found that cold treatment would induce flowering in all accessions tested, but only the biannual accession had a requirement for such a cold treatment, while the summer annuals could also be brought to flower by favorable light conditions alone[56]. As an interesting footnote to this work, Laibach points out that the work on the accession Warschau is incomplete, since this accession got lost in the turmoil of World War II – a testament to the working conditions at the time[56]. Later on, Laibach also added a publication on stratification of *Arabidopsis* seeds to induce and synchronize seed germination[57].

Following this early work on *Arabidopsis*, German plant geneticist Klaus Napp-Zinn decided to also adopt this new plant model to study the genetics underlying its vernalization responsiveness[58]. In **1957,** he published his studies on a cross between the natural accessions Limburg (Li) and Stockholm (St) that are early or late flowering, respectively[58]. Using genetic segregation analyses Napp-Zinn identified two main loci between the two accessions that confer the vernalization-requirement in St[58]. He named them *FRIGIDA* (*FRI*) and *KRYOPHILA* (*KRY*)[58]. In the following years, Napp-Zinn refined his analysis and confirmed his early findings, publishing a string of papers between **1957** and **1965**[59]. However, in the absence of any molecular biology and genomics tools, he eventually was unable to progress any further than having identified these two loci, thereby running into the same problem Chailakhyan had encountered when trying to identify florigen. Interestingly, when the first *Arabidopsis* meeting took place in Göttingen, Germany, in **1965**, the talks at the Symposium were transcribed and published as a supplement to the *Arabidopsis* Information Service newsletter[60]. Napp-Zinn delivered a talk regarding his progress on vernalization research since the 1950s, and the discussion following his presentation, which is included in the transcribed version, provides an interesting insight into the situation researchers found themselves in at a time when molecular biology did not yet exist and classical genetics had reached its limitations[61].

Around the same time, in **1960**, French botanist Pierre Chouard provided the first formal definition of '*vernalization*', as "*the acquisition or acceleration of the ability to flower by a chilling treatment*", which he included in his, at the time definite, review on the topic[62].

FLOWERING LOCI A, C, F & T, and the Emergence of *Arabidopsis* Natural Variation and Plant Epigenetics Research (1980 - today)

The big revival of vernalization research finally started in the mid-**1980s**, when the recent establishment of modern plant molecular biology techniques and the eventual adoption of *Arabidopsis* as a plant model organism opened countless new doors to plant researchers (see also 'A short history of *Arabidopsis thaliana* (L.) Heynh. Columbia-0', 'A short history of the CaMV 35S promoter' and 'A Short History of Plant Transformation'[42,63,64]).

In **1982** Caroline Dean had finished her PhD-studies in England and decided to join the American biotech startup Advanced Genetic Sciences Inc. for a postdoctoral position outside of academia[65]. To bring a bit of Europe with her into the new American home, Dean grew tulips in her apartment[65]. The observation that she had to place the tulip bulbs in the fridge for several weeks before planting them, intrigued her enough to read up on the process of vernalization[65]. She quickly realized that the underlying molecular mechanisms governing the vernalization response in plants were still not understood and so in **1987** decided to address this in a research proposal that got her a group leader position at the newly established John Innes Centre in Norwich, England[65]. In order to get started with her work, she visited Napp-Zinn in Germany, who, being semi-retired, was delighted that someone would carry on his work and happily provided Dean with seeds of his *Arabidopsis* crosses from the 1950s[65,66].

Building on Napp-Zinn's work, Dean and colleagues first set out to map the *FRI* and *KRY* loci[67]. By **1994** they had succeeded with the *FRI* locus, but were unable to map *KRY* to any specific position in the *Arabidopsis* genome[67]. Eventually, they concluded that the observed effects of *KRY* on the vernalization response were more likely caused by a combination of secondary effects, most prominently the growth conditions used, than a single locus or gene, and *KRY* therefore dropped out of vernalization research[67,68]. They mapped the *FRI* locus to a region on chromosome 4, indicating that *FRI* was allelic to *FLOWERING LOCUS A*, a locus indentified and mapped by the lab of Richard Amasino in 1993[67,69]. Still in 1994, it was furthermore found that the ability of the active *FRI* allele to repress flowering in winter annual *Arabidopsis* accessions (such as St) is dependent on the presence of an active allele at the *FLOWERING LOCUS C* (*FLC*)[70,71]. In Landsberg *erecta* (L*er*), no active *FRI* allele could be identified, which is due to the fact that L*er* does not carry this necessary active *FLC* allele[70]. The identification and mapping of these two key genes, *FRI* and *FLC*, meant a major breakthrough for vernalization research[72,73]. All of these observations, starting with Laibach's collection of natural *Arabidopsis* accessions, Napp-Zinn's work on the Li and St accessions, up to these comparative studies of the different accessions on a molecular level, can be regarded as early work on *Arabidopsis* natural variation - a research field that only really took off in the early 2000s and that work on vernalization has accordingly helped to launch[74]. Sadly, Klaus Napp-Zinn passed away in **1993**, just a year before his work finally helped in achieving this major breakthrough[66].

In **1999**, Michaels et al. and Sheldon et al. both demonstrated that *FLC* encodes a MADS-box protein that actively represses flowering[75,76]. *FLC* expression is positively regulated by FRI, and negatively by vernalization[75,76]. Furthermore, Sheldon et al. added that decreased genomic methylation also negatively regulates *FLC* expression[76]. This fit well with a 1993 observation by Burn et al. that non-targeted demethylation of the *Arabidopsis* genome induces early flowering[77]. This was followed in **2004** by two back-to-back publications on the molecular mechanism governing the silencing of *FLC* expression in response to vernalization[78,79]. Both, Bastow et al. and Sung et al., demonstrated that the *FLC* locus is dimethylated at two lysines in histone H3 following vernalization[78,79]. This histone methylation results in the repression of *FLC* expression, thereby allowing the plant to flower[78,79]. The activity of three VERNALIZATION (VRN) proteins is requires for this step, which are homologous to *Drosophila* Polycomb group proteins[78–80]. In *Drosophila*, these proteins were shown to be responsible for epigenetic gene silencing by chromatin modification, indicating that the VRN proteins could fulfill a similar function in plants[78–80]. Out of the *VRN* genes, *VRN1* and *2* are constitutively expressed, while *VRN3* expression is induced by cold treatment[79]. Thus, an active VRN1/2/3 polycomb-like repressive complex can only be formed in vernalized plants[79]. Accordingly, these two publication represent two of the earliest publications describing molecular details of an epigenetic gene regulation mechanism in plants, and vernalization research was therefore also vital in launching the emerging field of plant epigenetics[78,79].

Epigenetic effects had been observed since the 1950s, they just could not be explained at that time. They include the inactivation of one copy of the X chromosome in female mammals described in 1959/1961, to the varying pigmentation of corn kernels due to inheritable but reversible changes at the *R* locus in the maize genome in 1956/1960[81–84]. Alexander Brink used the word '*paramutation*' to describe these effects, while the term '*epigenetic*' was still occupied with a definition by Conrad Waddington from 1942[84,85]: Waddington referred to '*epigenetics*' as changes in gene activity in individual cells, caused by the cell's environment[85,86]. In his theory, a cell's environment would guide an undifferentiated cell towards a certain fate through external pressures – a concept that not coincidentally sounds very similar to Marxist-Leninist Dialectical Materialism[85,86]. In fact, Waddington considered Marxism a "profound scientific philosophy", and his definition of epigenetics was one result of him trying to integrate Marxism and biology[85,86]. Robin Holliday eventually slightly reframed Waddington's definition in 1987 to mean that epigenetics describes changes in gene activity during development[87]. He then updated this definition in 1994 to a more general 'study of the changes of gene expression', but added 'nuclear inheritance which is not based on differences in DNA sequence'[88]. By 1996, epigenetics and plant epigenetics were well on the way to being established as new fields of scientific research. An early plant epigenetics paper published in 1990 revealed that the silencing of a transgene under control of the Cauliflower mosaic virus 35S promoter was causally related to DNA methylation (see also 'A short history of the CaMV 35S promoter'[63])[89,90]. However, even at that time, books or special issues of journals related to this topic still had to start off with an attempt to finally provide a clear definition of the word[91,92]. A consensus definition was eventually published in **2009**, as ''An epigenetic trait is a stably heritable phenotype resulting from changes in a chromosome without alterations in the DNA sequence'[93].This definition, however, didn't really fit for vernalization[73]. Indeed, the silencing of *FLC* expression in response to vernalization is a '*phenotype resulting from changes in a chromosome without alterations in the DNA sequence*', and is also mitotically stable, but a **2008** paper by Candice Sheldon and colleagues clearly confirmed the previous observation that epigenetic silencing of *FLC* is reset in the next generation – therefore it is not '*stably heritable*' (which was one of the big lies of Lysenko)[75,94].Thus, it remains debatable whether the vernalization-dependent silencing of *FLC* expression is indeed an epigenetic effect, although it does appear that most researchers do consider it an '*epigenetic switch*'. In 2004, Richard Amasino argued: '*I think it is reasonable to refer to the vernalization-induced, mitotically stable acquisition of the competence to flower as an epigenetic switch because it is a change that can be propagated through cell divisions in the absence of the inducing signal*'[73].

Finally, FLC also connects flowering to a second pathway – that of the circadian clock and light. As described earlier, Gustav Gassner, Garner and Allard, as well as Mikhail Chailakhyan have all studied the control of flowering under different environmental conditions and found light conditions to play an important role. FLC connects these cold- and light-dependent pathways, by repressing the production of the FLOWERING LOCUS T (FT) protein, a locus that had been implicated in flowering already in **1991**[95–97]. In **1995**, the *CONSTANS* gene was identified as a regulatory protein promoting flowering under long-day conditions, since plants mutant for *co* would flower later under these conditions, whereas overexpression resulted in earlier flowering[98,99]. In two **1999** publications it was then revealed that CO acts via FT[100,101]. The exact mode of action of CO, and how it connects day length to flowering was subsequently unraveled between **2000** and **2005**[102–106]. The expression of *CO* itself is under control of the circadian clock[102,103]. Under long-day conditions, *CO* expression peaks at the end of the photoperiod, a time point that under short-day conditions already falls into darkness[102,103]. Light however, is a requirement for the CO protein to function since the CO protein is degraded in darkness, but stabilized by light[104]. So taken together, the expression of *CO* late in the day, and the requirement for light to stabilize the protein, means that active CO protein is only produced within a short temporal window of the day – and only under long day conditions with light late in the day[104]. In this short time frame, CO can activate FT to induce flowering[104]. However, both CO and FT were only found to be co-expressed in the phloem of leaves, which is not where flowers are formed[105,106]. Therefore, the last remaining question is: What is florigen, the mysterious substance theorized by Chailakhyan in 1936 that transmits the flowering signal from the leaves to the inflorescence? In **2007**, the groups of Phil Wigge and George Coupland both found that the FT protein itself is a mobile protein that translocates from the leaves to the inflorescence, where it then induces the transition to flowering[107,108]. Hence, the FT protein is the elusive florigen[107–109]. Mikhail Chailakhyan passed away in 1991, and, as is the case with Klaus Napp-Zinn, he did not see his pioneering work of this fascinating biological question come to a completion[53].

Further Reading:

- Pierre Chouard - Vernalization and its Relations to Dormancy[62]
- Valery N. Soyfer - The consequences of political dictatorship for Russian science[26]
- Ilya A. Zakharov - Nikolai I Vavilov (1887–1943)[15]
- Nils Roll-Hansen - Wishful Science: The Persistence of T. D. Lysenko's Agrobiology in the Politics of Science[28]
- Nikolay P. Goncharov, Nikolay I. Svel'ev - Ivan V. Michurin: On the 160th anniversary of the birth of the Russian Burbank[13]

- Richard M. Amasino - Vernalization, Competence, and the Epigenetic Memory of Winter[73]
- Charles Whittaker, Caroline Dean - The FLC Locus: A Platform for Discoveries in Epigenetics and Adaptation[72]

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