

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

4 A Short History of Vernalization

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9 Humans have known for centuries that some plants would only flower and produce yield in
10 late spring or summer if they are planted and germinated before winter¹. Such crop plants
11 display an enhanced cold tolerance, and survive through winter with the help of a protective
12 layer of snow, sheltering them from freezing¹. The benefit of growing such winter varieties is
13 that they produce higher yield than spring varieties¹. Importantly, such winter varieties don't
14 just tolerate winter weather – they actually require it, as they won't flower at all without this
15 period of cold¹. Today, this cold treatment is designated '*vernalization*'.

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

17 Around the year **1800** it was still a matter of debate what caused the difference in behavior
18 between spring and winter varieties of the same crop^{1,2}. According to John Lawrence, a
19 farmer and author of the 1800 '*New Farmer's Calendar*', '*it has been disputed, whether any*
20 *specific difference exists between spring and winter wheat*'². The question at the time was, if
21 these are actually different plants, or if their behavior was simply modified by their
22 environment². The latter would mean that it should be possible to 'train' them to behave
23 differently and adjust to a new environment¹. This was not so much an issue for farmers in
24 Europe and Asia, where wheat varieties had been grown for centuries and were bred to be
25 optimized for the local conditions^{1,3}. But the situation was different in the USA^{1,3}. Here,
26 wheat plants were imported from Europe, and some of the varieties that performed well in
27 their respective countries of origin, failed to do so when sown in the US^{1,3}. Especially in the
28 harsher climates of the northern states, this became a major issue^{1,3}. In the fertile Genesee
29 Valley in Flint, Michigan, for example, farmers failed to establish any of the most productive
30 imported European and Asian varieties, as they died off during the harsh winters^{1,3}. It was
31 only in the **1820s**, that a variety then known as Genesee Flint Wheat was established as a

32 successful variety^{1,3}. In this context, studying winter wheat suddenly became an important
33 issue, as plants that could survive under specific local conditions were urgently needed¹. In
34 **1860**, agriculturist John Hancock Klippart published his, at the time definitive book on '*The*
35 *Wheat Plant*', describing all the results and observations made by US farmers and
36 agriculturists over the past decades, when experimenting with different plants and conditions¹.
37 When it comes to winter and spring wheat, he also touches on the controversial topic of
38 conversion¹. Here, he describes that winter wheat could be transformed into spring wheat, and
39 vice versa, through a multi-generational adaptation process; one of the many attempts that
40 desperate farmers used to optimize their plants to the local environment¹. He describes how
41 few of the winter wheat plants will actually flower and ripen in the same year if they are
42 brought out in spring, and that they would be very weak and only yield moderate crop¹. If,
43 however, those seeds will be sown again in the following season, they would already grow
44 much better, and eventually, over several seasons, reach a productivity level equal to spring
45 wheat¹. Similarly, if spring wheat is sown out before winter, and if some plants would survive
46 the cold and frost, then the seeds of such plants will produce plants that will perform much
47 better in the following season¹. Another conversion experiment was conducted in **1837/38** by
48 Colonel Abbott, who reported his findings in *The Monthly Genesee Farmer*⁴. Abbott used
49 Flint winter wheat, which he soaked in a tub of water until sprouting⁴. At that point, he placed
50 the seedlings into a box, which he exposed to cold⁴. Eventually he sowed these seedlings out
51 in April and May, as one would do with spring wheat⁴. Those seedlings grew to full plants,
52 giving seed just as spring wheat would⁴. This experiment may therefore be the first
53 documented vernalization experiment⁴. While Klippart is generally supportive of these
54 *conversion* experiments, he is very critical of the so-called *transmutation* theory¹.

55 The transmutation theory describes a metamorphosis-like process, turning one plant into a
56 completely different one¹. A famous such 'pseudo observation', as Klippart calls it, was the
57 transmutation of wheat into *Bromus secalinus* ('chess' or 'cheat'), a rye-like weed¹.
58 According to supporters of the theory, the transmutation can be caused by either (I) excessive
59 moisture and cold in the spring months, (II) pasturing in the spring, or (III) hauling a wagon
60 over the field, transmutating every seed that get's squashed by the wheel¹. The prevalence of
61 this belief in the **1840s** eventually led Benjamin Hodge, an agriculturist and respected nursery
62 owner from Buffalo, New York, to offer a 100\$ reward to anybody, who could prove that
63 wheat was indeed transmuted into chess¹. For this, he worked with the New York State
64 Agricultural Society, who appointed a supervisory committee to evaluate the outcome of the
65 challenge¹. The 100\$ price was claimed by one Samuel David, who performed the following

66 experiment: He thoroughly cleaned wheat seeds to get rid of all chess contaminations¹. He
67 then germinated them in a pan, where he also subjected them to all possible harsh treatments
68 that would supposedly lead to transmutation (it is not documented if he wheeled a wagon over
69 the pan though)¹. He then sowed those seeds into regular soil, from where eventually not just
70 wheat, but also chess heads came up¹. Those seedlings were then presented to the
71 commission, showing some cases where the chess stalk seemed to indeed be emerging from a
72 wheat seed¹. However, careful microscopic investigation of the seedlings eventually
73 demonstrated that these stalks merely grew through or along the rotting wheat seeds, and *'the*
74 *examination therefore did not prove anything in favor of transmutation, and as there were*
75 *many possible ways in which the chess might have been scattered on the soil, the whole*
76 *experiment was admitted by all parties to be inconclusive'*¹. *'From hasty observations,*
77 *equally hasty inferences are generally made, and false conclusions are the result'*, Klippart
78 concludes¹.

79 There can be little doubt that the supporters of both, the conversion and the transmutation
80 theories, were heavily influenced by Jean Baptiste Lamarck's **1809** book *'Philosophie*
81 *Zoologique'*, which describes Lamarck's evolutionary ideas for the origin of species⁵. Those
82 ideas form the basis for Lamarckism – the dominant evolutionary theory at the time, prior to
83 the publication of Darwin's *'On the origin of species by means of natural selection (...)'* in
84 **1859**^{5,6}. *'Transmutation'*, according to Lamarckism, describes the evolution of complex
85 organisms from simple ones through the acquisition of required traits⁵. Basically, new traits
86 will evolve when they are needed, while existing traits may be lost if they are not actively
87 being used⁵. Once acquired, traits then become heritable through the generations, the
88 transmutation is complete⁵. Interestingly, the word *'transmutation'* was actually coined in
89 **1766** by German botanist Joseph Gottlieb Kölreuter, a pioneer in the field of plant sexual
90 reproduction and hybridization, who used the word to describe new breeds of plants that he
91 created via hybridization⁷.

92 Not surprisingly, no actual transmutations were ever reported in the following years, and the
93 transmutation theory was eventually abandoned. However, it did experience a revival in an
94 especially perfidious form in Soviet Russia, in the early 20th century, which will be discussed
95 here later. Actual research into the cold tolerance and cold requirements of different crop
96 varieties only seriously started after Klippart had published his book on the wheat plant in
97 1860.

98

99 **Cold Requirement Studies and Photoperiodism (1900 – 1927)**

100 The 20th century brought the first major scientific publication describing experiments with
101 different crop plant varieties to study their individual cold requirements⁸. In **1910**, German
102 botanist Gustav Gassner was given access to three large refrigerators at the Seed Research
103 Institute in Hamburg, Germany (Hamburgisches Botanisches Saateninstitut), with constant
104 temperatures at 1-2°C, 5-6°C or 12°C, a luxury at the time⁸. Using these refrigerators he
105 systematically tested plants for their response to these three different temperatures, length of
106 exposure to these temperatures and the developmental state during which the cold treatment
107 was applied⁸. He found that different plants do indeed require different temperatures to induce
108 flowering, that the temperature required can be linked to the developmental age of the plant
109 (i.e. older plants require colder or longer cold treatments), and that it doesn't need to be the
110 plant that is treated, but it can suffice to treat imbibed seeds⁸. Furthermore, he also discusses
111 that it is not just the temperature, but also other environmental factors that play a role⁸. These
112 factors include sugar content and, more importantly, light conditions – a very important point
113 still mostly overlooked at the time when studying flower induction⁸. Additionally, Gassner
114 even discussed a certain rhythmic pattern that plants seem to follow in their growth
115 throughout the year, thereby coming very close to describing photoperiodism⁸. He published
116 his extensive studies in a **1918** book, which triggered a boom in vernalization research for the
117 following decades^{8,9}. In fact, by the early **1930s**, the field was so well funded, that Gassner's
118 colleague Prof. August Seybold disparagingly labelled it '*Modelforschung*' (i.e. 'trendy
119 research')⁹. Gassner himself, however, could not benefit from this new trend⁹. Being an
120 outspoken opponent of the rising German Nazi-party and Adolf Hitler, he prohibited the
121 Hitler salute and any political activities in his institute, resulting in his removal from the
122 institute, imprisonment, and eventually his exile to Turkey in **1934**⁹. It was only in **1945**,
123 following the end of the Second World War, that he was again appointed as Rector and
124 Professor at his old Institute of Technology in Braunschweig, Germany⁹.

125 While Gassner already touched on the interconnectedness between cold treatment and day
126 length, it were Wightman W. Garner and Harry A. Allard who did the first extensive analysis
127 on the effect of day length on flowering time¹⁰. They exposed several plants to different day
128 length regimes and light intensities, and comprehensively described their individual light
129 requirements¹⁰. Regarding day length they confirmed that plants will only flower and set seed
130 if day length reaches certain limits, and that day length and cold temperatures are interrelated
131 to induce flowering^{10,11}. However, depending on the plant, long or short days could be

132 favorable for flowering. *'The term photoperiod is suggested to designate the favorable length*
133 *of day for each organism, and photoperiodism is suggested to designate the response of*
134 *organism to the relative length of day and night'*, they conclude in their work¹⁰. In their
135 follow up studies they even tried to 'localize' the response to day length within the plant^{11,12}.
136 They previously showed that *Cosmos bipinnatus* (Mexican aster) would not flower under
137 continuous light, but quickly under short day conditions^{11,12}. So to test if this is a local, or
138 general response, they exposed different branches of the same *Cosmos* plant to different day
139 lengths^{11,12}. And indeed, they were able to show that the branch exposed to winter day light
140 conditions quickly flowered, while the continuous light branch continued to grow
141 vegetatively^{11,12}.

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

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

147 Towards the end of the **19th century**, Ivan Vladimirovich Michurin, a railway worker from
148 central Russia, rose to become one of the most important figures in Russian agriculture¹³.
149 Michurin had cultivated fruit trees all his life in his parent's garden, and over the years this
150 hobby gradually developed into something bigger¹³. Despite his family being relatively poor,
151 Michurin spent all of his money on seeds and books about gardening and plant cultivation¹³.
152 His job with the railway enabled him to travel to all the famous gardens in central Russia,
153 where he studied the 'state of gardening' in his home country'¹³. Eventually, in the **1880s**, he
154 noted that *'after 15 years of comprehensive theoretical and practical studies of plant life and,*
155 *mainly, gardening and its needs in Middle Russia ... I have concluded that the level of our*
156 *gardening is too low'*¹³. He therefore took it onto himself to change this, founding a fruit tree
157 nursery in **1888**¹³. Over the course of the next five decades Michurin's nursery produced over
158 130 new varieties of fruit, such as apples, pears, cherries or plums¹³. He utilized a breeding
159 method based on distant hybridization, where he cross-pollinated distantly related plants in
160 order to produce new varieties¹³. For this, he developed several new techniques, including
161 methods to overcome incompatibility and even a primitive form of electroporation and
162 cytogenetics¹³. He also worked out novel selection processes to speed up this part of the
163 work¹³. Michurin published his studies in Russian horticulture journals and by the early **20th**
164 **century** he had authored around 100 scientific papers¹³. During this time, he tried to connect

165 with the Russian Department of Agriculture in order to receive funding for his research¹³. The
166 Department however, failed to see the value of Michurins work and merely offered him
167 smaller grants if he would conduct some experiments for them under their strict control,
168 which Michurin rejected¹³. However, while the Russian government did not realize the value
169 of Michurin's endeavors, they made sure that he did not strike a deal with the American
170 government either, which would have been happy to relocate him, his family and the entire
171 nursery to the US¹³. Michurin recalled later: '*higher spheres had prohibited me leaving for*
172 *America...*'¹³. He finally did get the recognition he deserved in 1920, following the Soviet
173 revolution, and with the help of Vladimir Lenin and another agronomist, Nikolai Vavilov¹³.

174 In the early **1900s** Nikolai Vavilov was the most important agronomist in the Soviet Union
175 and the Lenin-appointed director of the Lenin All-Union Academy of Agricultural Sciences¹⁴.
176 This basically put him in a position where he was responsible for the entire sector of
177 agricultural research in the Soviet Union^{14,15}. Vavilov was considered a pioneer not just in
178 Soviet Russia^{14,15}. Following his graduation from Moscow Commercial College in **1910**, he
179 entered the Moscow Agricultural Institute from where he received his PhD for his work on the
180 use of Mendelian genetics for the targeted breeding of more efficient crops¹⁵. He then joined
181 William Bateson at the John Innes Institute in the U.K., where he studied the resistance and
182 susceptibility of different wheat accessions from all over the world to fungal pathogens^{15,16}.
183 For this work he could apply his interest in studying the genetic diversity of the world's crop
184 plants to improve crop plant performance – a research program far ahead of its time^{15,16}. He
185 then continued his work as a lecturer and professor at the Saratov Agricultural Institute in
186 Russia until **1921**, when Vladimir Lenin personally appointed him as head of the Applied
187 Botany, and eventually director of the Lenin All-Union Academy of Agricultural Sciences¹⁵.
188 In this position, Vavilov emerged as one of the most important plant biologists of the 20th
189 century. In **1922** he published the influential law of homologous series in variation and
190 genetic mutability¹⁷. According to this, Vavilov argued, plant breeders should not try to
191 randomly breed better crop varieties, but look for beneficial phenotypic traits in closely
192 related plants (based on Carl Linneaus' work¹⁸), and then breed specifically for this trait – an
193 educated guess approach^{15,17}. He later added that homologous genes (based on Mendel's
194 work¹⁹), could be the basis for the observed phenotypic similarities¹⁷. Again, his work was
195 way ahead of its time. Knowing about the importance of genetic variability within plant
196 species, Vavilov then personally undertook or directed several expeditions to all parts of the
197 world to collect different natural accessions of the most important crop plants^{15,20,21}. He
198 analyzed these plants for their genetic and phenotypic diversity across the habitats from where

199 they were collected, arguing that the origin of a plant (i.e. the geographical region where
200 domestication started), would be the region of its highest diversity^{20,21}. Based on this theory,
201 he defined several ‘*centers of origin*’, such as the Middle East for different wheat, barley and
202 rye varieties, eastern Asia as the center of origin for soybean, rice or sorghum, and Central
203 America for maize and potato²⁰. He further extended and refined this monumental and
204 groundbreaking work between **1925** and **1933**^{20,22}. Moreover, he maintained and catalogued
205 all the seeds he collected on his travels around the world, creating the largest seed collection
206 for decades, with over 250.000 samples, representing the world’s diversity of food crops¹⁴.
207 The importance of this collection was re-confirmed when it was incorporated into the
208 Svalbard Global Seed Vault between **2005** and **2011**^{23,24}. And finally, in his role as director of
209 the Lenin All-Union Academy of Agricultural Sciences, Vavilov was also an outstanding
210 organizer. While in this position, he opened over 400 research stations and institutes
211 throughout the Soviet Union, thereby establishing the Soviet Union as a world leader when it
212 came to agricultural research, genetics and plant breeding¹⁴.

213 Following the **1917** October Revolution in Russia, the new Soviet Government immediately
214 seized all agricultural businesses, claiming them as national assets^{13,25}. Michurin’s nursery
215 was no exception to this¹³. However, Michurin, a supporter of the Soviets, was able to strike a
216 deal with the local land department, which recognized the value of Michurin’s work, therefore
217 allowing him to keep supervision of his nursery¹³. The district commissariat of agriculture
218 furthermore relayed the importance of Michurin’s work to The People’s Commissariat of
219 Agriculture, eventually garnering him the governmental recognition he deserved¹³. After that,
220 Vladimir Lenin personally promoted Michurin’s work publicly, further elevating his status¹³.
221 By **1920**, Vavilov was also aware of Michurin’s work and proposed to assemble a scientific
222 inventory of his nursery’s gene pool¹³. However, shortly after the Soviet’s seized power, the
223 Russian agricultural sector faced severe problems^{13,25}. Between **1925** and **1928**, harsh winters
224 with little or no snow had killed off the winter crops, resulting in severe yield losses and
225 famine^{13,25}. Stalin’s forced collectivization of agricultural farms resulted in inefficient and
226 mismanaged kolkhozes that dramatically decreased productivity^{13,25}. And on top of that,
227 Stalin’s purges resulted in the murder of some of the most productive farmers due to their
228 relative wealth, further decreasing agricultural production and, equally important, causing the
229 loss of crop varieties due to the subsequent mismanagement of the farms by Bolshevik
230 officials^{13,25}. Accordingly, one main objective for the agricultural scientists during that time
231 period became the breeding of new, better performing varieties of food crops^{26,27}. For this,
232 Vavilov decided on Michurin-inspired distant hybridization experiments, to breed better

233 performing cereal grain varieties²⁸. But one major problem that he encountered with these
234 experiments was the need to synchronize the different plants so that they would flower
235 simultaneously and could be cross-pollinated²⁸. At this point, the work of another young
236 scientist came to his attention²⁸.

237 Trofim Denisovich Lysenko was an agronomist, who in **1925** started to work on soil
238 enrichment at the Experimental Agricultural Station in Ganja, Azerbaijan²⁸. In the face of the
239 sustained famine in the country, however, he switched his focus to the conversion of winter
240 into spring wheat, to avoid the harsh winters²⁶. In his experiments, he basically repeated the
241 experiments that Colonel Abbott described in 1837: He soaked seeds in water and chilled
242 them at low temperatures for several weeks, before sowing them in late winter or spring^{28,29}.
243 As was the case for Col. Abbott, those seeds then germinated in spring and flowered in the
244 summer^{28,29}. In his **1928** publication describing these results Lysenko named this process of
245 cold treatment 'jarovization' (from jarovoe, the Russian name for spring cereals)^{28,29}. These
246 experiments came to the attention of Nikolai Vavilov, who figured that Lysenko's
247 jarovization could be a useful tool for him to synchronize the flowering of his distantly related
248 crops²⁸. He therefore invited Lysenko to speak at the **1929** national conference of agricultural
249 science in Leningrad, despite the fact that Vavilov's main expert in the field of plant
250 physiology, Nikolai Maksimov, was very critical of Lysenko due to his strong ego and
251 inability to take advice from colleagues²⁸. While Vavilov was only interested in jarovization
252 as a tool to synchronize flowering, Lysenko had much grander aims²⁸. At the conference, he
253 tried to sell jarovization as a tool to permanently transform winter wheat into spring
254 wheat^{28,30}. Despite this, Lysenko's presentation did not receive too much attention at the
255 conference, which didn't sit well with the ambitious scientist³⁰. In order to prove the
256 importance and applicability of his discovery, he planned a big publicity stunt²⁸. Together
257 with his peasant father, he jarovized lots of winter wheat seeds and sowed them out in
258 spring²⁸. In summer, the family's field was full of winter wheat, ready to be harvested²⁸. For
259 the rural community, this was close to a miracle, and accordingly this demonstration found
260 widespread coverage in local and national newspapers²⁸. On the back of this success, Lysenko
261 became known in Russia as a sort of miracle worker/scientist, and actually obtained his own
262 research laboratory at the Ukrainian Institute for Genetics in Odessa²⁸. There, he soon found
263 that mass jarovization of winter wheat was simply not practical to actually obtain a significant
264 increase in agricultural productivity, and he therefore switched his attention to jarovizing
265 spring wheat, arguing that it would ripen faster and produce more yield²⁸. But again, his
266 claims of a significant yield increase could not be confirmed in any scientific tests^{28,30}.

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

271 **Vernalization, Lysenkoism, and the 1948 Meeting of the Lenin All-Union Academy**
272 **(1931 – 1965)**

273 By **1931**, the situation in Russian agriculture had worsened even more^{28,30}. And now, the
274 government also started to directly interfere with academic research³⁰. Increasing pressure
275 from the Stalinist government to include Marxist ideology in the sciences, meant that the field
276 of genetics came under fire³⁰. Idealistically, Stalin's interpretation of nature was based on
277 Marxist-Leninist dialectical materialism^{27,31,32}. As such, nature had to be seen as a unified
278 whole, constantly developing according to guiding environmental pressures^{27,31,32}.
279 Accordingly, anything could be developed into any direction, if the correct pressure was
280 applied by shaping the appropriate environment^{27,31}. On a society level this means that a
281 classless society could be created if the right pressure was applied from above, and on an
282 individual level, that the Soviet government could (and should!) actively form its citizens and
283 their attitudes to become good Marxists and communists by creating the right environment
284 (i.e. the right pressure from above)^{27,31}. Evolutionary wise, this ideology borrows from
285 Lamarckism, in that new traits in an organism will constantly develop in order to resolve
286 existing constraints (pressures), and traits acquired this way would furthermore be inherited as
287 a 'state' of an organism^{27,31}. Thus, this ideology was to be adopted by the sciences as well²⁵.
288 As a plant-specific example: According to Lysenko, winter wheat, once jarovized, would
289 remain jarovized for the coming generations, having been pressured into becoming spring
290 wheat^{14,25}. Lysenko's work therefore fit very well into this ideology^{27,31}. Lysenko even went
291 as far as claiming that continuously plucking a leaf from a cotton plant, would eventually
292 result in leafless offspring²⁵. However, genetics and Darwinian evolution were considered
293 inconsistent with this Marxist-Leninist version of dialectical materialism³¹. Under this
294 situation of famine, starvation and increasing pressure to adhere to Soviet ideology, the
295 Communist party issued a **1931** decree that ordered agricultural researchers to create new and
296 more efficient crop varieties within the next 4-5 years²⁶. While the leading scientists protested
297 this unrealistic aim, Lysenko jumped at the chance to establish himself as a leader, and
298 claimed that using his jarovization technique, he would be able to breed such new varieties
299 within just two years²⁶. This promise, Lysenko's public reputation as a miracle worker, and

300 his publicly demonstrated willingness to bend the science to fit Marxist ideology, made him
301 Stalin's personal favorite, which would eventually result in the complete devastation of Soviet
302 agricultural sciences²⁶.

303 During this time, Lysenko and his jarovization also received some international recognition,
304 and in **1933**, the British Imperial Bureau of Plant Genetics published a bulletin focused on
305 Lysenko's work³³. In this bulletin, the latinized version of jarovization, '*vernalization*' (from
306 '*vernum*', latin for spring), is first used^{33,34}. But by **1935**, Lysenko had nothing positive to
307 present^{21,31}. He was not able to produce any new varieties, and all his work using jarovization
308 proved 'ineffective', as the 'successes' he reported were all based on falsified data and
309 accordingly were not reproducible by independent scientists^{21,31}. Lysenko reacted to these
310 failures with anger, claiming that his work and progress have been undermined by the other
311 leading scientists, explicitly naming Vavilov and their support of modern genetics^{21,31}. This
312 conflict between the two philosophies came to a head at the next congress of the Lenin
313 Academy of Agricultural Sciences in Moscow, in **1936**^{21,31}. Lysenko and his followers spoke
314 in support of Marxist-Leninist Dialectical Materialism, and heckled the other scientists, who
315 did their best to defend modern genetics and agricultural practices^{21,31}. Vavilov himself gave
316 two speeches during the Congress defending the application of Mendelian genetics and
317 Darwinian evolution, but eventually it became clear that Lysenko had the backing of Stalin,
318 and thus, the issue had already been decided^{21,31}. Vavilov lost his position as the Head of the
319 All-Union Academy of Agricultural Sciences, and in the following years several up-to-then
320 unknown authors published papers claiming that all of Vavilov's works were fraudulent,
321 including his work on the '*centers of origin*' and '*The Law of Homologous Series in*
322 '*Hereditary Variability*'²¹. Genetics, even the concept of the gene, Mendelian inheritance and
323 Darwinian evolution were subsequently considered reactionary and idealistic, even though
324 they were only formally outlawed in 1948. Lysenkoism took their place, despite Lysenko
325 preferring to call it 'Michurinist agrobiology'²⁷. Lysenkoism was based on Lamarckism and
326 the transmutation theory, but specifically adds that crops can also be 'trained' through
327 environmental pressure to behave in a certain manner^{27,35}. This included not just the
328 transmutation of winter into spring wheat, but even the transmutation of wheat into rye or
329 barley³⁵. Trying to capitalize on Michurins name and reputation, Lysenko claimed that
330 Michurin also bred his plants employing such a 'training' approach in line with party
331 ideology²⁶. Conveniently, Michurin had passed away in 1935, and was not able to defend
332 himself against this cooption²⁶.

333 In the following years, Lysenko continued to be criticized by his fellow Soviet scientists,
334 while Vavilov, despite being removed from his positions in the Academy, remained a highly
335 respected proponent of modern genetics¹⁴. As such, Lysenko realized that Vavilov would
336 always be a problem to his authority¹⁴. In **1940**, following a heated dispute between Vavilov
337 and Lysenko, Vavilov was arrested by agents of the People's Commissariat for Internal
338 Affairs. He was presented with charges of being a right-wing conspirer and spy for the British
339 Empire, and quickly convicted and sentenced to death¹⁴. While this sentence was eventually
340 commuted to 20 years of imprisonment, Vavilov died on January 26th, **1943**, of cardiovascular
341 failure and dystrophy, caused by starvation and sickness after several months in solitary
342 confinement¹⁴. ‘*We shall go to the pyre, we shall burn, but we shall not retreat from our*
343 *convictions*’, he had prophesized in 1939. Subsequently, he was declared a *persona non grata*
344 in Russia¹⁴.

345 For Lysenko, things only got slightly better following Vavilov’s removal. Criticism of
346 Lysenko, by then referred to as a ‘Dictator of Biology’, continued to mount in the absence of
347 any presentable results^{26,27}. By the time the important Meeting of the Lenin All-Union
348 Academy of Agricultural Sciences came closer in **1948**, Lysenko was forced to act. In the
349 lead-up to the meeting, Lysenko sent a letter to Stalin where he reassured himself of the
350 support from the Dictator^{26,27}. Simultaneously, he promised to produce a new wheat variety in
351 the coming year that would increase the countries wheat production tenfold^{26,27}. Together, the
352 two ‘dictators’ then carefully crafted and edited Lysenko’s speech for the meeting, which
353 aimed to once and for all silence the critics^{26,27}. Lysenko’s speech, entitled ‘*The Situation in*
354 *Biological Science*’, then took up the complete first day of the meeting^{26,27,36}. In it, Lysenko
355 spoke in favor of his Michurinist agrobiolgy, while speaking of modern genetics as
356 reactionary pseudoscience and a bourgeois perversion^{26,27,36}. As a consequence, the Politburo
357 officially prohibited the disciplines of modern genetics and Darwinian evolution, drafted a list
358 of laboratories that were to be shut down, and a list of scientists that were to be removed^{26,27}.
359 Overall, ‘*127 teachers, including 66 professors, were dismissed (...) the total number of those*
360 *(...) dismissed, demoted, or removed (...) amounted to several thousand*’²⁷. With this purge,
361 Lysenko had finally rid himself of all critics, and biological science was now completely
362 replaced with Lysenkoism³⁷. However, by the time of Stalin’s death in **1953**, Lysenkoism had
363 still not produced any real useful results³⁷. But since Lysenko had installed loyal followers on
364 virtually every important scientific position, no criticism was ever voiced publicly³⁷. Stalin’s
365 successor, Nikita Khrushchev, was similarly impressed by Lysenko as was his predecessor,
366 and he therefore remained in office³⁸.

367 While Soviet Russian plant science was totally under tight control by Lysenko, researchers in
368 other Soviet satellite states, such as Hungary and, even more so, Eastern Germany, still
369 enjoyed a certain amount of freedom in their work^{39,40}. The position of Eastern Germany was
370 unique in the sense that Berlin was not yet separated by the wall, which was first constructed
371 in 1961⁴⁰. Accordingly, if the Eastern German regime would have pressed the doctrine of
372 Lysenkoism onto its scientists too aggressively, they could simply have crossed the open
373 border into Western Germany (though the role of Hans Stubbe and others in the active
374 resistance against Lysenkoism must be mentioned as well)⁴⁰. In Hungary, in **1953**, György P.
375 Rédei, a young and talented plant biologist, was ordered by the Ministry of Agriculture to
376 confirm Lysenko's results^{39,41}. Specifically, he was asked to confirm the finding that winter
377 wheat could be transformed into spring wheat by vernalization, and that the vernalization state
378 would then be inherited in the future generations^{39,41}. Notably, he was not assigned to 'test'
379 Lysenko's claims, but explicitly to 'confirm' them³⁹. Not surprisingly, Rédei could not
380 substantiate Lysenko's results, and being a scientist of high integrity, he also published his
381 own results accordingly^{39,41}. Rédei's paper, published in Hungarian, was subsequently
382 translated into Russian and republished in the Russian journal *Izvestiya Akademii Nauk*
383 *SSSR*³⁹. However, when Rédei requested a back-translation into Hungarian, he found that the
384 journal's editor, Ivan E. Glushchenko, had altered his results so as to confirm Lysenko's
385 work³⁹. While Rédei was reportedly unhappy about this, this act may well have saved him
386 from punishment from the Hungarian Stalinist Rákosi Government³⁹. Only three years later,
387 in November **1956**, when Soviet tanks rolled into Budapest to violently squash a student
388 uprising against the communist dictatorship, Rédei and many of his fellow scientists
389 eventually fled the country and thereby freed themselves from the shackles and constant threat
390 of Lysenkoism³⁹. Taking with him a vial of *Arabidopsis thaliana* seeds he had just received
391 from Friedrich Laibach, Rédei became a temporary Assistant Professor for plant biology at
392 the University of Missouri, USA, where his work resulted not just in the establishment of the
393 Landsberg *erecta* and Columbia-0 *A. thaliana* lines, but also made him the 'Godfather of
394 *Arabidopsis* research' in the process (see also 'A Short History of *Arabidopsis thaliana* (L.)
395 *Heynh.* Columbia-0')^{39,42}.

396 Back in the Soviet Union, Lysenko's critics got louder once again in **1956**, when news of the
397 success of hybrid corn in the USA made it to Russia³⁵. In 1908, George Shull had described
398 his observation of hybrid vigor in a corn field, the fact that hybrids between two inbred lines
399 would appear more uniform and produce a higher yield than selfing within a single line
400 would^{43,44}. Research in the following years resulted in a rapid switch towards this approach to

401 create hybrid corn by farmers in the US⁴⁵. Lysenko however, disapproved of hybrid corn as he
402 considered it part of modern genetics^{35,45}. By the early 1950s almost all corn in the US was
403 hybrid, and the astonishing success made it obvious to the Russians that they were missing
404 out on a valuable discovery^{35,45}. This time, the resulting backlash Lysenko received for his
405 decision to ban hybrid corn was so strong that it actually forced him to resign as president of
406 the Academy of Agriculture³⁵. In the following years, Lysenko once again regained control of
407 the Academy of Agriculture with Khrushchev's help, but his authority was irreversibly
408 weakened following this revolt³⁵. Criticism again reached a boiling point in **1962**, when three
409 of the most prominent Soviet physicists, Yakov Borisovich Zel'dovich, Vitaly Ginzburg, and
410 Pyotr Kapitsa, presented a case against Lysenko, explicitly proclaiming his work as
411 pseudoscience^{27,35,46}. Following Khrushchev's dismissal as the First Secretary of the
412 Communist Party in **1964**, the president of the Academy of Sciences officially declared that
413 Lysenko's immunity to criticism was voided, and in **1965** he was finally removed from his
414 post for good³⁵.

415 While this episode in Russian history is now generally seen as a prime example of what can
416 happen when ideology is forced upon science, there are unfortunately still some revisionists
417 who try to paint Lysenko as an honest researcher who discovered vernalization and, in some
418 instances, laid the foundation for plant epigenetics³¹. These are a minority, however, and the
419 majority of people see Lysenko as the pseudo-scientist that he was³¹.

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

421 Curiously, one major breakthrough in understanding the mechanisms underlying the control
422 of flowering in plants was actually achieved in Soviet Russia during those troubled times⁴⁷.
423 Mikhail Khristoforovich Chailakhyan, a PhD-student in Moscow in the 1930s, was studying
424 photoperception in *Chrysanthemum*⁴⁷. He found that under short-day conditions
425 *Chrysanthemum* plants flower quicker than under long-day conditions, and then went on to
426 demonstrate that it was sufficient to expose the leaves to a certain light regime in order to
427 induce flowering⁴⁸. Therefore, it appeared to be possible to uncouple the locations of
428 photoperception (leaves) and response (inflorescence)⁴⁸. He then conducted subsequent
429 experiments, such as grafting the main stem of a long-day flowering plant onto the rosette
430 leaves of a short-day flowering plant, demonstrating that the long-day flowering stem would
431 now produce flowers under short-day conditions^{47,48}. These experiments led him to propose
432 that a substance produced in the leaves must exist, which then moves into the inflorescence
433 where it induces flowering^{47,48}. Believing that this substance might be a plant hormone, he

434 named it florigen ('blossom-former') in **1936**^{47,48}. As there was only one plant hormone
435 definitely described at the time - Fritz Kögl described and named auxin (greek for 'to grow')
436 in 1931 - Chailakhyan's finding promised to be a major breakthrough⁴⁷⁻⁴⁹. At the same time,
437 it is important to note that Julius Sachs already speculated in 1880 that a mobile leaf-produced
438 substance might be required to induce flowering, based on his earlier findings since 1863^{50,51}.
439 Chailakhyan presented his work as part of his thesis defense in **1938**, with Lysenko being part
440 of the committee⁵². Upon hearing this hormonal theory of plant development, Lysenko went
441 into a rage and attacked Chailakhyan's theory in '*broken, brief, and harsh phrases often*
442 *unconnected with each other*', as Chailakhyan remembered in 1988⁵². Plant development
443 guided by internal hormones was incompatible with Lysenkoism, claiming that plant
444 development is guided by the environment and external forces⁵². Chailakhyan was denied his
445 PhD, and in the following years was continually harassed and demoted from his academic
446 positions numerous times⁵³. But, while his supervisor Prof. Richter was dismissed from the
447 institute, Chailakhyan was able to stay and continue his research in low paying positions,
448 thanks to the help of several supporters who repeatedly rehired him every time he was fired⁵³.
449 Among those supporters was also Nikolai Vavilov, who had taken note of Chailakhyan's
450 talent and suggested to Lysenko that Chailakhyan could re-submit an edited version of his
451 thesis, that might appease both sides⁵³. This proposal was rejected by Lysenko⁵³. Chailakhyan
452 managed to stay in research until the end of Lysenkoism though, and finally picked up his
453 work on flowering time, trying to identify the substance that was his theorized florigen⁵³. He
454 eventually became one of the most famous Russian plant biologists, and a highly respected
455 member of the plant science community worldwide – staying active in research until his death
456 in 1991⁵³. Unfortunately, without the tools of modern molecular biology and biochemistry, he
457 was never able to identify florigen⁵³.

458 While all of this was going on in Soviet Russia, vernalization research in Germany did not
459 stop with the work of Gustav Gassner. Chailakhyan's work on florigen got German botanist
460 Friedrich Laibach interested in solving the mystery of what makes a plant flower⁵⁴. Or, in his
461 own words (*translated by me*), taken from the opening paragraph of his **1940** paper: '*If one*
462 *finds the plants in the rooms or on the balcony of a house to be in especially nice bloom, one*
463 *tends to compliment the housewife: 'you seem to have the right touch'. – therein lies the*
464 *confession though, that one does not really know what treatment is necessary to achieve this*
465 *blooming.*'⁵⁴. At the time, Laibach was already lobbying for the adoption of *Arabidopsis*
466 *thaliana* as a plant model organism and had built a collection of natural accessions that he and
467 his colleagues had collected all over Europe on their travels (see also 'A short history of

468 *Arabidopsis thaliana* (L.) Heynh. Columbia-0⁴²)⁵⁵. He now intended to use this collection to
469 analyze the flowering time of these accessions in response to different day lengths (he grew
470 them in a warm greenhouse as he did not take temperature into account yet)⁵⁴. He found that
471 all accessions flowered at one point, but that the flowering time varied dramatically; between
472 12 days post germination or only after the second year post sowing⁵⁴. He furthermore found
473 that the accessions from similar geographical regions also behaved similarly, specifically, he
474 found that the accessions from regions around the Mediterranean Sea seemed to require less
475 hours in light, while further north they required longer days, and the Scandinavian accessions
476 turned out to be biannual⁵⁴. He included the effect of temperature in his follow-up work in
477 **1951**⁵⁶. Here, he found that cold treatment would induce flowering in all accessions tested, but
478 only the biannual accession had a requirement for such a cold treatment, while the summer
479 annuals could also be brought to flower by favorable light conditions alone⁵⁶. As an
480 interesting footnote to this work, Laibach points out that the work on the accession Warschau
481 is incomplete, since this accession got lost in the turmoil of World War II – a testament to the
482 working conditions at the time⁵⁶. Later on, Laibach also added a publication on stratification
483 of *Arabidopsis* seeds to induce and synchronize seed germination⁵⁷.

484 Following this early work on *Arabidopsis*, German plant geneticist Klaus Napp-Zinn decided
485 to also adopt this new plant model to study the genetics underlying its vernalization
486 responsiveness⁵⁸. In **1957**, he published his studies on a cross between the natural accessions
487 Limburg (Li) and Stockholm (St) that are early or late flowering, respectively⁵⁸. Using genetic
488 segregation analyses Napp-Zinn identified two main loci between the two accessions that
489 confer the vernalization-requirement in St⁵⁸. He named them *FRIGIDA* (*FRI*) and
490 *KRYOPHILA* (*KRY*)⁵⁸. In the following years, Napp-Zinn refined his analysis and confirmed
491 his early findings, publishing a string of papers between **1957** and **1965**⁵⁹. However, in the
492 absence of any molecular biology and genomics tools, he eventually was unable to progress
493 any further than having identified these two loci, thereby running into the same problem
494 Chailakhyan had encountered when trying to identify florigen. Interestingly, when the first
495 *Arabidopsis* meeting took place in Göttingen, Germany, in **1965**, the talks at the Symposium
496 were transcribed and published as a supplement to the *Arabidopsis* Information Service
497 newsletter⁶⁰. Napp-Zinn delivered a talk regarding his progress on vernalization research
498 since the 1950s, and the discussion following his presentation, which is included in the
499 transcribed version, provides an interesting insight into the situation researchers found
500 themselves in at a time when molecular biology did not yet exist and classical genetics had
501 reached its limitations⁶¹.

502 Around the same time, in **1960**, French botanist Pierre Chouard provided the first formal
503 definition of ‘vernalization’, as "*the acquisition or acceleration of the ability to flower by a*
504 *chilling treatment*", which he included in his, at the time definite, review on the topic⁶².

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

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

512 In **1982** Caroline Dean had finished her PhD-studies in England and decided to join the
513 American biotech startup Advanced Genetic Sciences Inc. for a postdoctoral position outside
514 of academia⁶⁵. To bring a bit of Europe with her into the new American home, Dean grew
515 tulips in her apartment⁶⁵. The observation that she had to place the tulip bulbs in the fridge for
516 several weeks before planting them, intrigued her enough to read up on the process of
517 vernalization⁶⁵. She quickly realized that the underlying molecular mechanisms governing the
518 vernalization response in plants were still not understood and so in **1987** decided to address
519 this in a research proposal that got her a group leader position at the newly established John
520 Innes Centre in Norwich, England⁶⁵. In order to get started with her work, she visited Napp-
521 Zinn in Germany, who, being semi-retired, was delighted that someone would carry on his
522 work and happily provided Dean with seeds of his *Arabidopsis* crosses from the 1950s^{65,66}.

523 Building on Napp-Zinn’s work, Dean and colleagues first set out to map the *FRI* and *KRY*
524 loci⁶⁷. By **1994** they had succeeded with the *FRI* locus, but were unable to map *KRY* to any
525 specific position in the *Arabidopsis* genome⁶⁷. Eventually, they concluded that the observed
526 effects of *KRY* on the vernalization response were more likely caused by a combination of
527 secondary effects, most prominently the growth conditions used, than a single locus or gene,
528 and *KRY* therefore dropped out of vernalization research^{67,68}. However, the mapping of *FRI*,
529 and the subsequent finding that *FRI* function is dependent on a second locus, named
530 *FLOWERING LOCUS C (FLC)* (also referred to as *FLOWERING LOCUS F (FLF)*, and
531 identified simultaneously in the labs of Maarten Koornneef, Richard Amasino and Caroline
532 Dean), eventually meant a giant leap forward for vernalization research^{67,69–72}. Sadly, Klaus
533 Napp-Zinn passed away in **1993**, just a year before his work finally helped in achieving this

534 major breakthrough⁶⁶. The function of the active *St. FRI* allele to repress flowering in winter
535 annual *Arabidopsis* accessions is dependent on the presence of an active *FLC* allele^{69,70,72}. In
536 Landsberg *erecta* (*Ler*), no active *FRI* allele could be identified, which is due to the fact that
537 *Ler* does not carry the necessary active *FLC* allele⁶⁹. All of these observation, starting with
538 Laibach's work on his collection of natural *Arabidopsis* accessions, Napp-Zinn's work on the
539 Li and St accessions, up to the comparative studies of different accessions on the molecular
540 level in the 1990s, can be regarded as early work on *Arabidopsis* natural variation, a research
541 field that only really took off in the early 2000s and that work on vernalization has helped to
542 launch⁷³.

543 In **1999**, Michaels et al. and Sheldon et al. both demonstrated that *FLC* encodes a MADS-box
544 protein that actively represses flowering^{74,75}. *FLC* expression is positively regulated by *FRI*,
545 and negatively by vernalization^{74,75}. Furthermore, Sheldon et al. added that decreased
546 genomic DNA methylation also negatively regulates *FLC* expression⁷⁵. This explained a 1993
547 observation by Burn et al. that non-targeted demethylation of the *Arabidopsis* genome induces
548 early flowering⁷⁶. Following these findings, the Dean lab published on the molecular
549 mechanism governing the silencing of *FLC* expression by DNA methylation in response to
550 vernalization⁷⁷. In their **2004** study, Bastow and colleagues demonstrate that the *FLC* locus is
551 dimethylated at two lysines in histone H3⁷⁷. This methylation step involves the activity of two
552 proteins homologous to *Drosophila* Polycomb group proteins, which were shown to be
553 responsible for epigenetic gene silencing by chromatin modification^{77,78}. Accordingly, this
554 publication represents one of the earliest publications describing molecular details of an
555 epigenetic gene regulation mechanism in plants^{77,78}. Therefore, vernalization research was
556 subsequently vital in helping to launching the emerging field of plant epigenetics too⁷⁷.

557 Epigenetic effects had been observed since the 1950s, they just could not be explained at that
558 time. They include the inactivation of one copy of the X chromosome in female mammals
559 described in 1959/1961, to the varying pigmentation of corn kernels due to inheritable but
560 reversible changes at the *R* locus in the maize genome in 1956/1960⁷⁹⁻⁸². Alexander Brink
561 used the word '*paramutation*' to describe these effects, while the term '*epigenetic*' was still
562 occupied with a definition by Conrad Waddington from 1942^{82,83}: Waddington referred to
563 '*epigenetics*' as changes in gene activity in individual cells, caused by the cell's
564 environment^{83,84}. In his theory, a cell's environment would guide an undifferentiated cell
565 towards a certain fate through external pressures – a concept that not coincidentally sounds
566 very similar to Marxist-Leninist Dialectical Materialism^{83,84}. In fact, Waddington considered

567 Marxism a "profound scientific philosophy", and his definition of epigenetics was one result
568 of him trying to integrate Marxism and biology^{83,84}. Robin Holliday eventually slightly
569 reframed Waddington's definition in 1987 to mean that epigenetics describes changes in gene
570 activity during development⁸⁵. He then updated this definition in 1994 to a more general
571 'study of the changes of gene expression', but added 'nuclear inheritance which is not based
572 on differences in DNA sequence'⁸⁶. By 1996, epigenetics and plant epigenetics were well on
573 the way to being established as new fields of scientific research. An early plant epigenetics
574 paper published in 1990 revealed that the silencing of a transgene under control of the
575 Cauliflower mosaic virus 35S promoter was causally related to DNA methylation (see also 'A
576 short history of the CaMV 35S promoter'⁶³)^{87,88}. However, even at that time, books or special
577 issues of journals related to this topic still had to start off with an attempt to finally provide a
578 clear definition of the word^{89,90}. A consensus definition was eventually published in **2009**, as
579 "An epigenetic trait is a stably heritable phenotype resulting from changes in a chromosome
580 without alterations in the DNA sequence"⁹¹. This definition, however, didn't really fit for
581 vernalization⁹². Indeed, the silencing of *FLC* expression in response to vernalization is a
582 '*phenotype resulting from changes in a chromosome without alterations in the DNA*
583 *sequence*', and is also mitotically stable, but a **2009** paper by Ruth Sheldon and colleagues
584 clearly demonstrated that the epigenetic silencing of *FLC* is reset in the next generation –
585 therefore it is not '*stably heritable*' (which was one of the big lies of Lysenko)⁹³. Thus, it
586 remains debatable whether the vernalization-dependent silencing of *FLC* expression is indeed
587 an epigenetic effect, although it does appear that most researchers do consider it an
588 '*epigenetic switch*'. In 2004, Richard Amasino argued: '*I think it is reasonable to refer to the*
589 *vernalization-induced, mitotically stable acquisition of the competence to flower as an*
590 *epigenetic switch because it is a change that can be propagated through cell divisions in the*
591 *absence of the inducing signal*'⁹².

592 Finally, *FLC* also connects flowering to a second pathway – that of the circadian clock and
593 light. As described earlier, Gustav Gassner, Garner and Allard, as well as Mikhail
594 Chailakhyan have all studied the control of flowering under different environmental
595 conditions and found light conditions to play an important role. *FLC* connects these cold- and
596 light-dependent pathways, by repressing the production of the FLOWERING LOCUS T (FT)
597 protein, a locus that had been implicated in flowering already in **1991**^{94–96}. In **1995**, the
598 *CONSTANS* gene was identified as a regulatory protein promoting flowering under long-day
599 conditions, since plants mutant for *co* would flower later under these conditions, whereas
600 overexpression resulted in earlier flowering^{97,98}. In two **1999** publications it was then revealed

601 that CO acts via FT^{99,100}. The exact mode of action of CO, and how it connects day length to
602 flowering was subsequently unraveled between **2000** and **2005**¹⁰¹⁻¹⁰⁵. The expression of *CO*
603 itself is under control of the circadian clock^{101,102}. Under long-day conditions, *CO* expression
604 peaks at the end of the photoperiod, a time point that under short-day conditions already falls
605 into darkness^{101,102}. Light however, is a requirement for the CO protein to function since the
606 CO protein is degraded in darkness, but stabilized by light¹⁰³. So taken together, the
607 expression of *CO* late in the day, and the requirement for light to stabilize the protein, means
608 that active CO protein is only produced within a short temporal window of the day – and only
609 under long day conditions with light late in the day¹⁰³. In this short time frame, CO can
610 activate FT to induce flowering¹⁰³. However, both CO and FT were only found to be co-
611 expressed in the phloem of leaves, which is not where flowers are formed^{104,105}. Therefore, the
612 last remaining question is: What is florigen, the mysterious substance theorized by
613 Chailakhyan in 1936 that transmits the flowering signal from the leaves to the inflorescence?
614 In **2007**, the groups of Phil Wigge and George Coupland both found that the FT protein itself
615 is a mobile protein that translocates from the leaves to the inflorescence, where it then induces
616 the transition to flowering^{106,107}. Hence, the FT protein is the elusive florigen¹⁰⁶⁻¹⁰⁸. Mikhail
617 Chailakhyan passed away in 1991, and, as is the case with Klaus Napp-Zinn, he did not see
618 his pioneering work of this fascinating biological question come to a completion⁵³.

619

620 **Further Reading:**

- 621 - Pierre Chouard - Vernalization and its Relations to Dormancy⁶²
- 622 - Valery N. Soyfer - The consequences of political dictatorship for Russian science²⁶
- 623 - Ilya A. Zakharov - Nikolai I Vavilov (1887–1943)¹⁵
- 624 - Nils Roll-Hansen - Wishful Science: The Persistence of T. D. Lysenko's Agrobiology
625 in the Politics of Science²⁸
- 626 - Nikolay P. Goncharov, Nikolay I. Svel'ev - Ivan V. Michurin: On the 160th
627 anniversary of the birth of the Russian Burbank¹³
- 628 - Richard M. Amasino - Vernalization, Competence, and the Epigenetic Memory of
629 Winter⁹²
- 630 - Charles Whittaker, Caroline Dean - The FLC Locus: A Platform for Discoveries in
631 Epigenetics and Adaptation⁷¹

632

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