Mini-review
DOI 10.1007/s12038-010-0035-1

The conversion of spring wheat into winter wheat and vice versa: false claim or Lamarckian inheritance?

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Paul Kammerer, an Austrian biologist, argued strongly in favour of the Lamarkian view on the inheritance of acquired characters. In his most controversial experiment, Kammerer forced midwife toads, which live and mate on land, to mate and lay their eggs in water. Most of the eggs died, but a few (3–5%) of offspring that survived had lost the terrestrial habits of their parents and, by the third generation, they began to develop black nuptial pads on their forelimbs, a character common to water-dwelling species. This experiment is often cited as an example of scientific fraud. Recently, however, Vargas (2009) has re-examined Kammerer's midwife toad experiments and argues that these experiments show signs of epigenetic inheritance. An immediate discussion on this topic has been published in a recent issue of *Science* (Pennisi 2009). This new analysis reminds us of several recent reports on the inheritance of acquired behaviour adaptations and brain gene expression in chickens, which may have been transmitted to the offspring by means of epigenetic mechanisms (Lindqvist *et al.* 2007; Natt *et al*. 2009). It especially reminds us of Trofim Lysenko's converted wheat, a situation exactly analogous to Kammerer's midwife toad.

The characteristic of winter wheat is that if sown in the spring it fails to form ears. It has been shown that the capacity to form ears depends on the plant's passing through a definite internal qualitative change. It was Lysenko who coined the term jarovization, which was later translated into vernalization. It is defined as 'the acquisition or acceleration of the ability to flower by a chilling treatment'. The characteristic feature of winter wheat is its requirement of rather low temperature for vernalization. The usual duration of the process of vernalization in most winter wheat at low temperatures (0°–10°C) is 30–50 days, depending upon the variety. Once this stage has been accomplished, the plant becomes capable of forming flowers in favourable conditions. Spring wheat differs from winter wheat in that it does not require vernalization, and is thus able to ear when sown in spring. Winter and spring habit, as a Mendelian character transmitted by gametes, is a hereditary property in wheat. Before 1930, Lysenko had shown that vernalization of winter wheat can be accomplished before it is sown. The process is to allow the grains to take up water and swell, and then to keep them for the required time at a temperature of 0–3°C. The grains are then dried off: they show no signs of germination but when subsequently sown in spring they ear normally, indicating that they have passed the phase of vernalization. This treatment has no effect on the hereditary behaviour of the plants. That is to say, the progeny of the pre-vernalized spring-sown wheat is still winter wheat; if sown (without pre-vernalization) in the following spring it will not form ears (Morton 1951; Lysenko 1954).

However, in a series of experiments carried out between 1935 and 1940, Lysenko and his colleagues established that permanent changes in heredity can be induced by appropriate changes in external conditions at the critical period of vernalization. In the earliest experiments, winter wheat was sown in the greenhouse and kept at a temperature higher than the temperature required for vernalization in normal conditions. After 152 days, 30–40% of the plants eared and gave ripe seed, indicating that these plants had succeeded in completing the vernalization stage, although very slowly, at the higher temperature. The seeds were sown and raised again in the same conditions. This time the plants eared in 77 days. A third generation was raised in the same way and gave ears at 46 days. The seed from the three generations that had passed the vernalization stage at the higher temperature was then sown in the field. The experimental plants behaved as spring forms and eared, but the control plants from the original seed material did not ear at all. Lysenko suggested that the later stage of vernalization was the critical period, in which the change would become hereditarily fixed. Thus, concretely, to change winter wheat

Keywords. Epigenetic inheritance; Lamarckian inheritance; Lysenko's converted wheat; vernalization

to spring wheat, vernalization should begin at the normal low temperature but complete the last stages at a higher temperature. It should be noted that Soviet workers have also carried out many experiments on the reverse change from spring wheat to winter wheat. The method is to sow spring grains in the autumn. In these conditions, usually 30–40% of the plants successfully survive the winter and form grain. After two to three overwinterings in this way, seed obtained when sown at the normal early autumn sowing date gives a high proportion of winter-hardy plants. When tested by sowing in spring, a high proportion of the seed is found to possess the winter character, that is, it will not form ears, showing that it has acquired the requirement of low temperature for vernalization (Morton 1951; Lysenko 1954).

It is well known that Vavilov was a distinguished Soviet geneticist and one of the strongest opponents of Lysenko. However, historical studies have shown that Vavilov played the chief role in Lysenko's scientific advancement. In September 1931, at a meeting of the State Commissariat for Agriculture, Vavilov said: 'Of especial interest … is the work of Lysenko, who has actually managed in practice to change late-ripening into early-ripening strains and to convert winter into spring varieties. The facts which he has established are indisputable and are of considerable interest … Lysenko's experiments show that, with special pre-sowing treatment, late Mediterranean varieties of wheat may be converted into early varieties in our conditions. Many of these varieties surpass our ordinary varieties in quality and productivity … Rapid organizational collective persistent work is required in order to realize the most interesting facts established by Lysenko' (Soyfer 1989). At the 6th International Congress of Genetics, Vavilov (1932) said: 'The remarkable discovery recently made by T D Lysenko of Odessa opens enormous new possibilities to plant breeders and plant geneticists of mastering individual variation. He found simple physiological methods of shortening the period of growth, of transforming winter varieties into spring ones and late varieties into early ones by inducing processes of fermentation in seeds before sowing them.'

It should be noted that the conversion of winter wheat into spring wheat and *vice versa* that Lysenko described was not a new discovery. Lysenko failed to mention the names of his predecessors in his publications, thus many people (including Vavilov) mistook this for a new discovery. Actually, in the nineteenth century, several researchers had observed this fact. For example, Darwin (1868) mentioned Monnier's experiments in which winter wheat was sown in the spring and spring wheat in the autumn to produce spring or winter wheat, respectively: 'He sowed winter-wheat in spring, and out of one hundred plants four alone produced ripe seeds; these were sown and resown, and in three years plants were reared which ripened all their seed. Conversely, nearly all the plants raised from summer-wheat, which was sown in autumn, perished from frost; but a few were saved and produced seed, and in three years this summer-variety was converted into a winter-variety.' By comparing Darwin's records with Lysenko's experimental result, one can find that a major difference between the observations made by Monnier and those by Lysenko is the percentage of offspring that acquired the new characters. While in the first case it is only about 4%, Lysenko reports about 30–40%. The main reason is that the frequency of conversion is determined by the variety (genotype), suitable sowing time and other conditions. For example, Rajki (1967) showed that the percentages of converted wheat in certain lines during the first year were 6–10% and, in later years, 58–77%.

The evidence for the conversion of spring wheat into winter wheat and *vice versa* still remains highly controversial: the wider community would probably say that it is false. Over the past several decades, however, the conversion of spring wheat into winter wheat and *vice versa* has been repeatedly carried out at dozens of experimental stations in the Soviet Union (Sergeev 1955; Lysenko 1958; Zaruballo 1958; Trukhinova 1960, 1966; Remeslo 1962; Glavinich 1963; Khitrinsky 1963; Fedorov 1966; Glushchenko *et al.* 1972; Krivogornitsyn 1978; Dolgushin and Taran 1983; Movchan and Krivobochek 1985; Zhivotkov *et al.* 1990). Their experimental results were confirmed by some non-Soviet researchers in Hungary, Bulgaria and China (Enchev 1957, 1979; Li 1964; Rajki 1985). There were about 200 papers on conversion between spring and winter wheat during 1930s and 1980s (Rajki 1985). Many new varieties were produced by this conversion method. For example, in their trials during 1985–1989, Zhivotkov *et al.* (1990) selected 437 lines; 85 of them were produced by converting spring to winter forms. The winter wheat variety 'Mironovskaya 808', which was converted from the spring wheat 'Artemovka', had been cultivated over many millions of hectares (Rajki 1985). The first Bulgarian varieties of winter two-rowed malting barley were produced from spring varieties by repeated late sowing in the autumn (Enchev 1979). The outstanding wheat breeder Maksimchuk regarded the conversion of spring to winter forms as a breeding method equally as valuable as hybridization (cited in Rajki 1975). Glushchenko (1979) considered the conversion of winter to spring forms as a method for creating high-productivity spring wheat varieties.

Here we would like to cite the carefully controlled and ten years' work involving three cycles of conversion of spring into winter wheat by Sandor Rajki, the former director of the Agricultural Research Institute of the Hungarian Academy of Sciences and a full member of the Hungarian Academy of Sciences. His initial stock was Lutescens 62 and lines derived from it, all of which were shown to be genetically pure non-hardy spring wheat and, by means of repeated autumn sowing, these could be gradually converted into winter wheat. He emphasized that four successive autumn sowings were necessary for conversion into a winter type. If the four autumn sowings were interrupted by one spring sowing in the third season, the original spring habit was hardly altered (Rajki 1967). In reply to some people's criticisms, he argued that his method of pedigree selection was on a single-plant basis which, combined with isolation, progeny tests and genetic analysis, ensured that the experimental material was homozygous, instead of contamination. This gradual 'adequate' change cannot be regarded as being due to spontaneous mutation (Rajki 1969). His results of the experiments and theoretical viewpoints had already been published in various papers, and his lectures were delivered at scientific meetings in Europe and North America (Rajki 1965, 1966, 1967, 1969, 1975, 1985). Commenting on this study, Professor Agaev of Leningrad noted: 'All in all the autumnization research carried out by Rajki deserves the highest praise, as the data arose from experiments with a strictly applied methodology' (cited in Bedo 2007).

The success of conversion depends upon the variety (genotype), suitable sowing time and other conditions (Didus 1957; Rajki 1966). For example, Driga (1963) summarized his work on the conversion of spring durum and soft wheat varieties into winter hardy forms. Of the 20 varieties used in the experiment, only 7 varieties were successfully transformed. Priilinn (1960) reported that the spring wheat Kauka was readily converted into a winter wheat by repeated autumn sowings, Diamant was difficult to be transformed and took a longer time, and German wheat 31243 did not alter at all after four years' autumn sowings. In general, the conversion did not occur immediately and more than two generations are necessary for the conversion from spring to winter wheat. Remeslo (1962) showed that soft spring wheat must be sown in autumn for at least two generations to accomplish conversion into winter wheat, while this process requires at least four generations in durum spring wheat. Glushchenko *et al*. (1972) demonstrated that the conversion of winter wheat into spring wheat took place gradually and was complete after five generations of spring sowing. According to Lysenko (1958), when the spring wheat Milturum 321, Odessa 13 and Lutescens 1163 were sown for two successive years early in the autumn (late August or early September), their progeny contained a higher proportion of converted winter plants than when sown in late autumn. Similar results were achieved by Omarov (1958) and Karapetyan (1964).

The mechanism underlying the conversion of winter and spring wheat into each other remains unclear. Lysenko (1963) proposed that any change in the heredity of an organism is adequate; that is, it corresponds to the influence of the changed environmental conditions which it has assimilated (cited in Rajki 1985). The characteristic feature of winter wheat is its requirement of rather low temperature for vernalization. If the temperature is completely outside the required range, vernalization will not take place and the plant will not form ears. If, however, conditions are such that slow or partial vernalization takes place and is completed at a temperature higher than its critical requirement, then the normal course of metabolism at the critical phase is disturbed. Such a disturbance is transmitted to the germ cells and causes what Lysenko called de-stabilized or shaken heredity. The progeny will have a greater capacity to adapt themselves to a higher temperature for completion of the vernalization phase. If sown in the spring so that they 'assimilate' the higher temperature, the new adaptive capacity will be fixed as a new hereditary requirement for higher temperature, and the winter wheat becomes a spring form. It is an essential part of Lysenko's conception that the new adaptive capacity resulting from shaken heredity can become fixed only by the action of the appropriate external conditions, acting if necessary over several generations. It should be noted that Rajki (1967) believed that it is possible for an environmental factor to exert an influence, which occasionally causes a change in the DNA sequence and fixes the changes genetically. Unfortunately, this is not supported by any molecular data.

In recent years, genetic studies comparing winter and spring wheat have identified three genes (*VRN1*, *VRN2* and *VRN3*) in the vernalization response. The *VRN1* gene is a meristern identity gene and is dominant for spring growth habit. Reduction of *VRN1* transcript levels by RNA interference results in a delay in flowering of 2–3 weeks, suggesting that the transcript level of *VRN1* is critical for the determination of flowering time in wheat. The *VRN2* gene is a zinc finger CCT transcription factor and is dominant for winter growth habit. This gene is downregulated by vernalization, releasing the transcription of the *VRN1* genes and promoting flowering. Mutations in the CCT domain or deletions of the *VRN2* gene are associated with a spring growth habit (Yan *et al.* 2004; Dubcovsky *et al*. 2007). Current models of flowering regulation in wheat suggest that, before vernalization, *VRN3* is repressed by *VRN2.* Vernalization results in the upregulation of *VRN1* and the downregulation of *VRN2* in the leaves. The release from *VRN2* repression results in higher transcript levels of *VRN3* and the promotion of *VRN1* above the threshold levels required for flower induction (Distelfeld *et al.* 2009).

There has been increasing evidence that vernalization results in DNA demethylation that induces flowering. Winter wheat is more highly methylated than spring wheat (Sherman and Talbert 2002). It has been widely accepted that vernalization-induced flowering is an epigenetic phenomenon (Minorsky 2002; Amasino 2004; Bastow *et al.* 2004). Epigenetic effects are often heritable, in the sense that they are passed on from one cell generation to the next.

Epigenetic variations can also be transmitted from parents to progeny (Jablonka and Raz 2009). It is not unreasonable to postulate epigenetic mechanisms that could plausibly result in the conversion of spring to winter wheat or *vice versa*, although this would require new and carefully controlled experiments using the currently available molecular tools that were not available at the time these experiments were done. It would be extremely interesting if someone did try to repeat the conversion experiments and hypothesize how epigenetic modification of some of these *VRN* genes could possibly explain the observed conversion.

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MS received 29 December 2009; accepted 15 April 2010

*e*Publication: 6 May 2010

Corresponding editor: Vidyanand Nanjundiah