ESTRATTO

Articles

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Was Lysenko (Partly) Right? Michurinist Biology in the View of Modern Plant Physiology and Genetics

Key words. Heritability, Lysenko, Punctuated equilibrium, Somatic mutations, Directed mutations, Sir Sebright's effect, Frozen plasticity, Evolution.

Abstract. *Soviet Lysenkoism was the darkest period of modern science, and its main product – Michurinist biology – was a collection of absurd theories usually based on anecdotal observations or on a few badly designed experiments without proper controls and without any statistical evaluation of results. However, in the thirties and early forties, Lysenkoists also described (and misinterpreted) some interesting data and observations which could have been real and which might inspire modern biologists to construct testable hypotheses and suggest experiments that could extend our scientific knowledge. Here, I attempt to present an explanation in terms of modern biology of some of those phenomena, namely vegetative hybridization, wobbled heritability, heritability of environmentally induced adaptive modifications and effects of intravariety hybridization of self-fertilizing cultivars. The first two phenomena can be explained on the basis of visualization of hidden*

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genetic and epigenetic polymorphism (originating from somatic mutations, somatic recombination and paramutations), the third phenomenon by the occurrence of intraindividual selection of somatic cell lines, and the fourth phenomenon by low heritability of phenotypic properties (and therefore also low capability to evolve) of outcrossing organisms (in comparison with self-fertilizing or asexual organisms), i.e., by a theory of frozen plasticity.

1. INTRODUCTION

The term Lysenkoism is usually used to denote the political, social and prerogative activities of Lysenko and his followers which resulted in practical destruction of whole branches of science and carriers, and often even lives, of scientists in the Soviet Union and partly also in its political satellites. The roots and impacts of these persecutions have been thoroughly analyzed (Medvedev [1969]; Roll-Hansen [1999]). The term Lysenkoism, however, has also a second meaning: a genetic and evolutionary theory, termed "Michurinist biology" or "Soviet creative Darwinism" by its proponents, promoted by Lysenko and his followers from the early thirties to the late sixties. Michurinist biology is based on the assumption of completely "soft" heredity. Properties of organisms should be easily influenced by the environment, and the environmentally induced changes should be (and mostly would be) transmitted genetically to the offspring. These ideas were in contradiction with the body of knowledge of standard genetics even in the thirties. Although we can suspect that the primary motif of Lysenkoists' decision to abandon classical genetics in favor of a "new and better" (i.e., "progressive and proletarian") genetics was to replace "official" geneticists in their posts in the scientific management, we cannot exclude the possibility that Lysenko's views could have been influenced by his agrotechnical experience. Although Lysenko's empirical evidence supporting his theory would not stand critical review by nowadays' (or even his time's) standards (Medvedev [1969]), we cannot a priori exclude the possibility that some of the described phenomena were real and only the insufficient scientific knowledge of Lysenko and his co-workers caused that they were misunderstood and misinterpreted.

I would like to provide an explanation of some phenomena described by Lysenko, which might be compatible with the tenets of modern biology. I would intentionally neglect the possibility that these phenomena never occurred and that the results were fabricated by Lysenko or his co-workers. In the late thirties, Michurinist genetics coexisted with standard Mendelian genetics, and therefore the chance of forgeries was lower than after the official triumph of Lysenkoism in the forties. I will therefore focus my attention especially on the older papers included in "Agrobiology", the basic textbook of Michurinist genetics (Lysenko [1950]). In particular, I will concentrate on the problems of vegetative hybridization, wobbled heritability, heritability of environmentally induced adaptive modifications and positive effects of intravarietal hybridization of self-fertilizing plant cultivars.

2. VEGETATIVE HYBRIDISATION

Vegetative hybridization (grafting) in plants has been always appreciated by plant-breeders as a powerful tool for production and propagation of interspecies hybrids (with low or null fertility) and of rare recombinants with useful properties. Michurinists, however, claimed that vegetative hybridization could be used also for many other purposes. They asserted that young branches grafted on an old tree of a different sort or even species acquire some properties of the stock, and that some of such acquired properties can be sexually transmitted into next generation. For example they maintained that a branch of a tomato variety with yellow fruit, grafted on a red fruit tomato variety, provided some fruits with a reddish tint, and some plants grown from the seed of these reddish-tint fruits gave yellow, reddish and occasionally red fruits (Lysenko [1950], p. 279-280, 405). As Lysenko did not fail to stress out, "assimilates" but not chromosomes from the stock can enter the scion. Similar experiments have been repeated with the same results in the sixties and seventies by Japanese authors (Hirata [1979], [1980a], [1980b]).

How could one presently explain this phenomenon without assuming the theoretically possible but not very likely participation of retroviruses transferring genes from stock into a scion? It is not very surprising that the properties of stock influence epigenetically the properties of the scion. Not only low molecular weight molecules but also proteins and RNA can easily move through phloem and therefore also enter from the stock into the scion (Crawford and Zambryski [1999]). Current experience with transgenic plants shows that regulation of gene expression is integrated across the whole body of a plant (Jorgensen *et al.* [1998]; Kooter *et al.* [1999]): overproduction of a transgene product in one part of a plant often results in gene inactivation (e.g. by a methylation of regulatory sequences of the gene) in all tissues of the transgenic plant. The red colour of tomato fruits in experiments of Michurinists and the Japan authors, however, has been transmitted to the next generation by seeds. Today we know that individual organs and tissues of a plant do not have to be genetically identical. Genomes of their cells might differ due to somatic mutations, somatic recombination (results of relatively common mitotic crossing over), or due to hereditable (but often reversible) modifications (e.g. methylations) of the genome (Otto and Hastings [1998]). Under normal conditions biochemical differences between parts of a plant are very difficult to observe because transported molecules synthesized in other parts of the organism influence both ontogeny and physiology (and therefore phenotype) of a particular plant tissue. If a branch of a tomato plant has a genetic predisposition to produce reddish instead of yellow fruits, we might be unable to recognize it, as the pigment intermediates or pigment-synthesizing enzymes, or the gene expression regulators are mixed due to mobility of molecules within the whole plant (Crawford and Zambryski [1999]). The same branch grafted on a red-fruit tomato may obtain some of these molecules from the stock; therefore at least some fruits may be reddish, and we may be able to select the fruits with the highest predisposition for a red color. The procedure of grafting and selection of most reddish fruits can be repeated several times (as was described by Lysenko), until we finally obtain a plant that gives red fruits through seed reproduction.

3. WOBBLED HERITABILITY

Visualization of hidden genetic polymorphism could have played a role also in the production of organisms with "wobbled heritability" (Lysenko [1950], pp. 289, 335, 415-417). According to Lysenko's definition, heritability is the ability of a living body to demand for its development specific conditions and react to these or different conditions in a specific way. Therefore, growing the plants under conditions which they are not used to (for example out of their normal geographic range), can result into development of plants with so called "wobbled heritability" that could be then used e.g. for breeding of new varieties. While the normal range provides the plants with just the conditions demanded for normal development, the foreign range provides alien conditions, and the plants react to them in an abnormal way. The nature of these individual reactions is often heritable, i.e., could be transmitted to the offspring.

What used to be called "wobbled heritability" could well be the visualization of hidden genetic polymorphism, this time, however, at the level of a population. Current molecular biology clearly shows that a large fraction of genes in populations is polymorphic; they exist in any given population in several relatively common forms (Kreitman and Akashi [1995]). Large part of this polymorphism is hidden under normal conditions, i.e., it does not contribute to observable phenotypes (Mayr [1963]). Under abnormal conditions, however, some hidden polymorphisms may manifest at the level of phenotypes of individual organisms in the population (Imasheva *et al.* [1999]). The intrapopulation variability sharply rises. A variance of quantitative traits increases, and forms of qualitative traits that are absent or extremely rare under normal conditions appear. Observed "homogeneity" of populations under normal conditions is at least partly caused by "genetic canalization", genetic and epigenetic processes which can mask an influence of genetic differences among individual organisms at the phenotype level (Stearns and Kawecki [1994]; Waddington [1942], [1959]; Wagner *et al.* [1997]; Wilkins [1997]). The best-known process contributing to genetic canalization is genetic dominance, the ability of a dominant allele to mask the presence of a recessive allele.

Phenotypical expression of many genes is also affected by epistasis, i.e., by activity of modificators, genes that influence the extent of out-manifestation of alleles in other loci (Martin and McGowan [1995]; Nanjundiah [1993]). Due to complex and often rather indirect nature of their action, the modificators may work properly only under normal conditions, i.e., in the environment in which they were originally selected for. Under abnormal conditions many of these genes-modificators have lower capacity to mask the genetic differences, the hidden polymorphism becomes apparent and produces phenotypic polymorphism that could be used in selecting organisms with new properties.

4. HERITABILITY OF ENVIRONMENTALLY INDUCED ADAPTIVE CHANGES IN PLANTS

Certain categories of results described in the Lysenkoist literature suggest the existence of a phenomenon only rarely accepted by modern biologists, namely the possibility of a heritable adaptation of individual organisms to local conditions in organisms lacking the Weissmann barrier (e.g. in plants) by the mechanism of an intraindividual selection of somatic cell lines. For example, the outcome of vegetative hybridization was substantially dependent on the age of the donor of the scion. A branch (even a young one) originating from an old tree remains stable and provides fruits with properties of the donor, while a branch from a young tree acquires the properties of the stock and produces fruits with changed properties (Lysenko [1950], p. 223; Michurin [1952], p. 22-23).

Plant age was also claimed to play a role in pollen compatibility. A young tree (sometimes only in its first season of fertility) can be fertilized with pollen from foreign varieties (or even species), while the spectrum of potential pollen donors for the same tree in next seasons becomes much narrowed (Michurin [1952], p. 28-29; Turbin [1952], p. 198). Hybrids of two different garden varieties of perennial cabbage provide in the first season seeds which give hybrids with combinations of properties of both parents, in the next seasons the same plants produce hybrids more and more similar to kale, the original wild parent of both garden varieties (Turbin [1952], pp. 188-189).

Even more important was the observation concerning the influence of environmental conditions on heritable properties of plants. Many plants are self-incompatible – they cannot be fertilized by their own pollen. Pollen incompatibility extends also to clones obtained from the same individual by vegetative reproduction (e.g. by cutting a stool or a bulb). According to Michurinists, this incompatibility within the clone can be evaded if two clones of the same plant are grown in divergent conditions (e.g., one in dry, one in moist) (Turbin [1952], p. 138).

To explain such results we must accept the possibility of existence of frequent genetic or stable epigenetic changes in the somatic tissues of plants (Otto and Hastings [1998]). The relatively rare (and undirected) "traditional" mutations are a rather unlikely candidate. A far more feasible source of such changes may be paramutations, i.e., programmed and often reversible modifications of regulatory elements of genes (Itoh *et al.* [1997]), or somatic recombination due to crossing over between two homologous chromosomes during a normal mitotic cycle. Unlike meiotic recombinations, somatic recombinations occur many times during the life of individual plant. In somatic recombinants, total DNA content remains unchanged, while the context of some genes changes, as some sequences from chromosomes of paternal origin are exchanged for homologous sequences from chromosomes of maternal origin. This can result in a phenotypic change of the recombinant cell and its progeny due to the so-called position effect (Henikoff [1992]; Tartof [1994]; Kleinjan and van Heiningen [1998]), i.e., a change in gene activity caused by changes in cis-acting elements in the vicinity of affected genes. Somatic recombinations can result in gradual breakdown of well-tried combinations of genes (i.e., linkage groups of genes, supergenes (Bishop *et al.* [1981])) during the life-span of a hybrid plant (which can explain the result of cabbage experiment). From the point of view of general biology more important is the fact that hereditary differences in the phenotype exist between cells of different parts of a single plant. These differences can serve as a basis of intraindividual competition and selection. Individual cell lines (and therefore individual branches) might be more or less adapted to the existing conditions, which could result in differences in growth rates or differentiation competency of these lines. In the latter stages of the plant life only cell lines best adapted to the local conditions will participate in the development of germinal organs. Also the resistance of different apical meristems to local adverse conditions (which may manifest itself in the efficiency of pollen and fruit production) may vary within the plant. This could be a principle underlying genotrophs and similar phenomena recognized by nowadays' botany (Cullis [1973], [1984]) and also the heritable adaptations in plants described (and misinterpreted) by Michurinists.

Let's now return to the problem of pollen incompatibility between clonal plants grown under same conditions, and compatibility between the same plants grown under dissimilar conditions. Regardless of the stochastic nature of somatic recombination, the selection operating on cell lines and its results are more or less determined by environmental conditions. Therefore, the genetic (and epigenetic) information of germinative cells of two plants developed in identical conditions will be more similar to each other than that of two plants developed under dissimilar conditions. Such intraindividual selection-induced (both genetic and epigenetic) differences between clonal plants grown under dissimilar conditions can result into an improvement of pollen compatibility.

It is worthwhile to mention here that the same phenomenon, which I suggest to call "Sir Sebright's effect", can operate at the level of populations. Charles Darwin in his intraspecies variability-book (Darwin [1868], Part II, pp. 115-117, 143) discussed a phenomenon of gradual long-term deterioration of beneficial properties of pure races of domestic animals. He cited Sir John Sebright who had claimed that this process could be prevented and even reverted by crossing the animals with those of the same race from herds reared under dissimilar conditions. At the face value, it is difficult to explain the existence of Sir Sebright's effect in terms of mainstream genetics and the recommendation (ignored by modern scientists but widely followed by breeders) to cross genetically related animals reared under dissimilar conditions seems to be rather bizarre. However, if we take into account the possibility of different conditions selecting for different alleles, the recommendations of Sebright, Darwin and others can be considered quite reasonable.

5. INTRAVARIETAL CROSSING OF SELF-FERTILIZING PLANTS

Intravarietal crossing of self-fertilizing plants was originally recommended by Lysenko for wheat varieties, later the same technique was tried also with other species of self-fertilizing plants. Lysenko pointed out that, in contrast to varieties of rye (outcrossing plant), the varieties of self-fertilizing wheat were highly unstable, gradually losing their beneficial properties. Many established varieties of rye are being cultivated for long time on large areas, while most of the varieties of wheat disappear from fields and from catalogues of seed companies within thirty years (Lysenko [1950], pp. 105, 111). According to Lysenko, old varieties of wheat must be continuously substituted by new ones because the self-fertilizing plants are unstable and their good properties (for which they have been originally selected) are getting lost during long-term cultivation. He claimed that this process can be stopped and reverted by artificial outcrossing between the plants of the same variety.

Although this technique seems to be groundless at first glance, it could be a mistake to reject the idea without closer examination. Current theoretical views suggest the existence of a large difference in evolutionary plasticity between sexual and asexual organisms. While the asexual (and more or less also the self-fertilizing) organisms can easily evolve under selection pressure by a classical Darwinian mechanism, the same is not true for sexual species (Wright [1931]; Mayr [1963]; Dawkins [1982]). The primary obstacle for evolution by natural selection is a low heritability of biological fitness (Dawkins [1982]), and often also low heritability of polygenic traits (Flegr [1998]). The fitness of an organism is determined by its phenotype. However,~~ the~~ influence of parti~~cular ph~~enetic traits on fitness is highly “context specific”, i.e., the same trait in the context of certain traits can be useful, in the context of other traits harmful. Similarly, the influence of a particular gene on the phenotype is often context specific (this time genotype-context specific). Due to epistatic interactions between genes, the effect of an allele on the phenotype depends on the context of the alleles of other genes (Wright [1931]; Mayr [1963]; Kanavakis *et al.* [1982]; Wainscoat *et al.* [1983]). In asexual organisms the genotype of organisms is transmitted between generations in an unchanged form. Therefore, a particular allele has the same influence on the phenotype (and fitness) of both parent and progeny. In sexual outcrossing organisms, the genotypes of offspring arise every generation "de novo" by mixing genes from two parents. Therefore, the same allele (mutation) occurs in every generation in the context of a different genotype, and its influence on the phenotype and fitness might dramatically differ. It makes the evolutionary response of sexual species on selection pressure difficult. While asexual (and partly self-fertilizing) populations are as a rule evolutionarily plastic for the whole time of their existence, the populations of sexual species are plastic only under conditions of low genetic polymorphism (when alleles occur in every generation in the same or very similar context) (Flegr [1998]). Such situation occurs for example after a bottleneck-including speciation event (Carson and Templeton [1984]; Templeton [1980]) or in experiments with small or inbred populations (Goodnight [1987]; Bryant *et al.* [1986]; Whitlock *et al.* [1993]). Under normal conditions, the response of a population to selection is only slow and mostly transient, i.e., after termination of the selection and breeding program the phenotypes return toward original values. The frozen plasticity of sexual species can be responsible for observed coupling of anagenesis with speciation, i.e., for punctual nature of evolution of most multicellular species in paleontological record (Gould and Eldredge [1993]).

The self-fertilizing varieties of wheat are evolutionarily plastic for the whole duration of their existence. Therefore, they can gradually collect mutations that increase their fitness but at the same time decrease their agricultural value. On the other hand, outcrossing varieties of rye have much lower capability to evolve, since the same mutation occurs in every generation in a different context, therefore its selection coefficient can oscillate between positive and negative values. To prevent deterioration of a rye variety, we only need to avoid contamination by pollen (or seeds) from foreign varieties. On the other hand, a variety of wheat (or of other self-fertilizing plant) must be continuously subjected to a selection pressure for its useful properties, or it must be from time to time substituted by a new variety. Theoretically, it might also help to prepare seed for sowing by forced outcrossing (as has been recommended by Lysenko), although one may doubt the economical feasibility of this procedure.

6. EPILOGUE

The theories of Lysenkoists are so crazy that their experiments nobody else has repeated, and their reputation is so bad that no well-informed and decent scientist is willing to read their works. Despite this, interesting data and observations that might inspire a biologist to construct testable hypotheses might be concealed in the body of Michurinist literature. It is rather an ethical problem whether the scientific works of criminals should be ignored or not. It should be, however, argued that by avoiding the topics and the areas of science that were in the center of attention of these people we actually allow them to shed malice even long after their physical or political death.

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LYSENKO AVEVA (IN PARTE) RAGIONE? LA BIOLOGIA MICIURINISTA ALLA LUCE DELLA MODERNA GENETICA E FISIOLOGIA VEGETALE

Riassunto

Il Lysenkoismo sovietico può essere considerato uno dei periodi più tragici nella storia della scienza moderna e il suo principale prodotto, la biologia Miciurinista, un insieme di teorie assurde, solitamente basate su osservazioni aneddotiche o su pochi esperimenti mal impostati, privi di controlli adeguati e di verifiche statistiche dei risultati. D'altro canto, negli anni '30 e '40 i Lysenkoisti riportarono, e interpretarono erroneamente, alcune interessanti osservazioni che potrebbero riferirsi a fenomeni reali e da cui potrebbero trarre ispirazione i biologi moderni. Abbiamo presentato una spiegazione in termini di moderna biologia di alcuni di questi fenomeni, ovvero l'ibridazione vegetativa, la ereditarietà "traballante", l'ereditarietà di modificazioni adattative e l'ibridazione tra diverse varietà di cultivars riproducentesi per autofecondazione.