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Epigenetic Mechanisms Regulating Seed Germination Rate

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Abstract—Changes in epigenetic polymorphism degree within wheat seedlings' population under radiation stimulating exposure of germination were investigated. Variations in seeds sample allocations by germination rate in both control and chronically exposed variants were estimated. Changes in DNA methylation patterns of seedlings from seeds with different germination rate were studied. Variations in epigenetic polymorphism – "distance" between DNA methylation patterns of "fast" and "slow" seedlings of different wheat varieties under radiation exposure were assessed. Indicated, that increased germination rate of seeds sample was associated with decreasing degree of epigenetic polymorphism. Issue concerning both role of epigenetic polymorphism in plant population stability and its decreasing degree that could initiate less effectiveness of production process was discussed.

Keywords: seed germination, stress, chronic exposure, DNA methylation, epigenetic polymorphism

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INTRODUCTION

Seed germination is one of the key stages in the harvest formation. Therefore, the mechanisms that determine this process are under the attention of the modern selection and biology of production process [1, 2]. In recent decades, various methods of germination stimulation have been proposed [2–7] that are based on the empirically selected dose for each type and variety of cultivated plants and exposure mode of the stress factor. Currently, presowing radiation exposure and hydropriming are the most investigated and implemented [2–5]. The use of the priming phenomenon in practice claims the requirements for the results' reproducibility and molecular markers' detection that allows one to prognose both the result of stress exposure and its maintenance time [8, 9]. The answers to these questions are in the plane of determining of the "memory" mechanisms that cause these effects, identifying interactions of different regulation levels that determine the stimulation effects (hormesis) and adaptation.

There are a number of theoretical developments and hypotheses explaining the phenomenon of seed germination stimulation by certain doses of stress factors. One of the first explanations of radiation stimulation on germination, along with other hormesis effects of "small doses," is an increasing yield of free radicals and reactive oxigen species [3, 5]. It was assumed that these factors play the role of triggers that remove physiological calm and enhance transcriptional activity. The expansion of the ideas about regulatory processes hierarchy that determine responses to abiotic stresses has led to the explanation of the phenomenon of priming by a stable change in the level of key metabolites of signaling systems or transcription factors [8–10]. The hypothesis of stress-induced epigenetic modifications, which play a possible role in long-term changes in gene expression, has been formulated [10]. Thus, a wide range of issues related to the effect of germination stimulation, as well as other hormesis and adaptation occurrence, and their connection with the regulation of gene expression, kinetic characteristics, influence on the subsequent organism life activity, cause scientific interest but remain underexplored.

In the previous studies, a connection between the variation in the seed germination rate of one species, variety, and crop, with the polymorphism of the DNA methylation pattern of plants originating from them, has been established [11]. It is also shown that the differences in methylation pattern of fast- and slow-growing seedlings are associated with their different resistance to abiotic factors and to the adaptive capacity [12, 13]. The quantitative polymorphism evaluation observed between methylation pattern of fast- and slow-growing seedlings of different wheat varieties [14] revealed a positive rank correlation between this index and variety's ecological plasticity, which had low sensitivity to the seeding time, fertilization, and pesticide treatment. The data set points to the existence of an epigenetic mechanism that determines the nonsynchronism of seed germination and the polymorphism maintenance in the population by the seeding time as one of the mechanisms of resistance and adaptation of plant population.

The aim of the work was to identify changes in the epigenetic polymorphism associated with the stimulation of seed germination under gamma radiation exposure.

MATERIALS AND METHODS

Studies were carried out on the winter wheat cultivars Podolyanka and Favoritka, whose originators are the Institute of Plant Physiology and Genetics of the National Academy of Sciences of Ukraine collaborative with the Cherkasy Institute of Agroindustrial Production.

A comparative analysis of the germination kinetics was based on the evaluation of two indices: the relative germination rate of the seeds, i.e., the proportion of seeds ($N_i - N_{i-1}/N$) germinated between the $i - 1$ and the i hour from the swelling onset, and the cumulative curve, i.e., the total proportion of seeds germinated to the i hour from the swelling onset,

$$\sum (N_i - N_{i-1}/N),$$

where N is the total sample size.

Sample sizes were determined in accordance with the statistical analysis rules, according to which the sample sizes should be at least 300–400 variants for construction and determination of the distribution type [15]. The group of fast-growing (FG) seeds did not exceed 35–40, and slow-growing (SG) did not exceed 25–30. Seeds were germinated in a germinating chamber on the trays with moistened filter paper at 22–23°C. To conduct studies of seedlings' DNA methylation, a group of FG seeds were selected from control and exposed seed samples after 12 h of swelling onset, and SG seeds were selected after 24 h. The experiment was repeated seven times. The source of chronic gamma exposure of the seeds was a glass container with a $^{137}CsCl$ solution, the dose rate was 12.9 μA/kg, and the accumulated dose was 3.2 Gy.

Statistical analysis was carried out using the MS Office Excel software.

DNA was isolated from 11–12-day-old wheat seedlings using a Diatom™ DNA Prep100 reagent kit based on NucleoS sorbent (Ukraine).

PCR was carried out on a Tercyck thermal cycler (DNA Technology, Russia). Primers RAPD P6 (GAG–CAA–GTT–CAG–CCT–GG), ISSR 5'-$(AC)_8$C-3', and primers to the transcribed DNA sequences (Metabion, Germany) were used [11, 12]. A set of GenPak® PCR Core reagents, lyophilized dry mixtures ready for DNA amplification, were used for the PCR.

The 20 μL ISSR–PCR reaction mix contained 1 U of Taq polymerase inhibited for "hot start," 10 μL of buffer, 2.5 mM of $MgCl_2$ and 200 μM of each dNTPs, 0.1 μM of primer, 200 ng of total genomic DNA, 6.4 μL of deionized water. The mixture was coated with 20 μL of vaseline oil. Amplification program with ISSR and RAPD-P6 primers included an initial denaturation of 5 min at 94°C followed by 40 cycles: denaturation at 94°C for 45 sec, primer annealing at 52°C for 45 sec, and elongation at 72°C for 90 sec. The final elongation continued for 7 min at 72°C [16, 17].

The DNA restriction with subsequent amplification was also carried out on a Tercick thermal cycler (DNA Technology, Russia). Two restriction enzymes were used: MspI (5'–CC*CGC–3') and MboI (5'–C*CGC–3') (Fermentas, Lithuania). The restriction reaction with the MspI enzyme was performed in a total volume of 25 μL, which contained 0.6 U enzymes, 2 μL 10× buffer Tango, 500 ng total genomic DNA, and 17.1 μL deionized water. The mixture was coated with 20 μL of vaseline oil.

The restriction reaction for MboI enzyme was performed in a total volume of 25 μL, which contained 0.2 U of the enzyme, 2 μL of 10× buffer Tango, 500 ng of total genomic DNA, and 17.7 μL of deionized water. The mixture was also coated with 20 μl of vaseline oil.

Conditions for restriction reactions were: 16 h at 37°C, reaction termination for 20 min at 65°C (for MboI) and 20 min at 80°C (for MspI).

The restriction and PCR products were separated in a 1.0% agarose gel with TBE buffer stained with ethidium bromide and visualized on a UV transilluminator. The same volume of PCR products (5 μL) was applied in each electrophoresis slot. A molecular-weight size marker GeneRuler 50 bp DNA Ladder (Fermentas, Lithuania), with fragments of length 1000, 750, 500, 250 and 50 bp, was used.

The DNA methylation patterns from the sample of the FG seedlings were compared with the DNA pattern of the SG seedlings. Comparison of the DNA methylation revealed polymorphism of two seedling groups, evaluated be means of epigenetic distance index (D), which was calculated using the Nei approach modification [18]. According to this, if X and Y are two electrophoretic spectra representing a set of amplicons of the restriction products, then x_i and y_i are the frequencies of the common bands of this set. The probability of the identity of the randomly chosen bands was $j_X = \sum x_i^2$ for the set X, and $j_Y = \sum y_i^2$ for the set Y; the probability of the bands identity for the set X with the band from the set Y was $j_{XY} = \sum x_i y_i$. The normalized identity of the bands between X and Y was evaluated as,

$$I = \frac{J_{XY}}{\sqrt{J_X J_Y}},$$

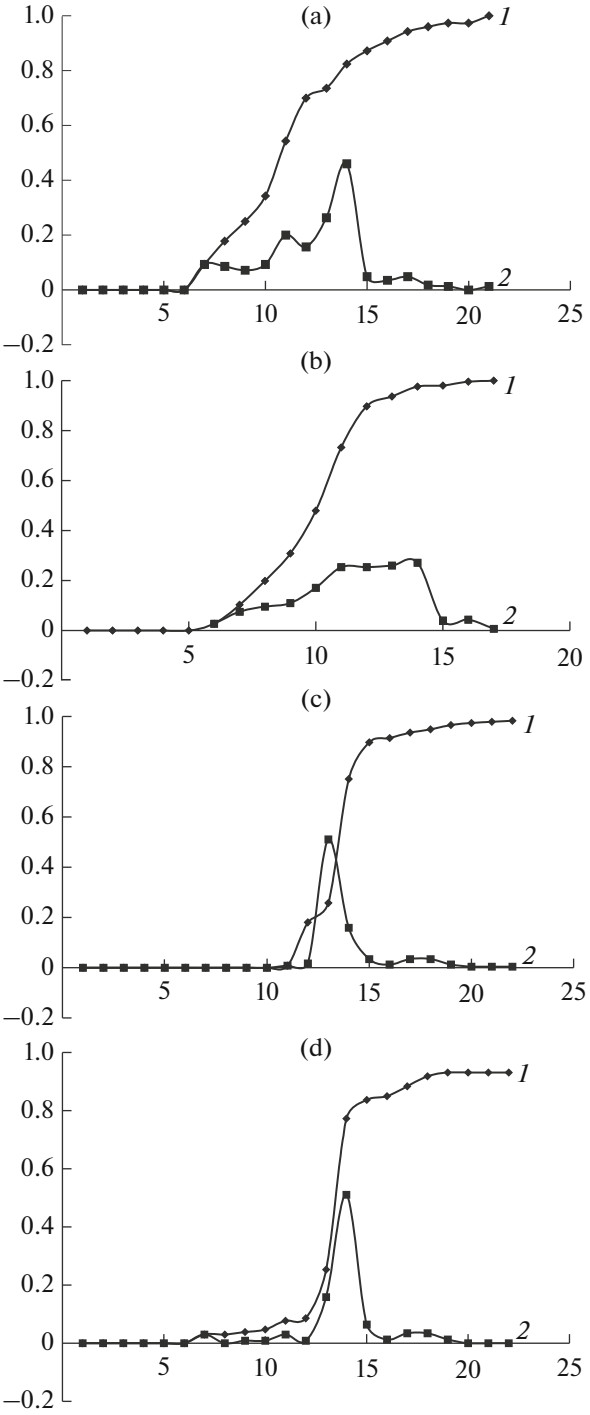

Fig. 1. Cumulative dependency (1) and distribution according to the relative germination rate (2) of wheat seed samples of the (a, b) Podolyanka and (c, d) Favoritka cultivars: (a, c) control, (b, d) chronic radiation exposure. Vertically—relative units; horizontally—duration of swelling, h.

where J_X, J_Y, and J_{XY} are the arithmetic means of j_X, j_Y, and jXY, respectively. The difference between the electrophoretic spectra, the so-called as epigenetic distance between samples X and Y, was $D = -\ln I$. In this case, $D = 0$ with an absolute coincidence of the band set in the compared electrophoretic spectra and $D = 1$ when the whole set of amplicons in electrophoretic spectra are different.

RESULTS AND DISCUSSION

Germination kinetic studies indicated that, in both control and chronically exposed samples, distribution of the seed sample according to the germination rate depending on the swelling onset time did not correspond to the normal distribution and the cumulative curve was not S-shaped (Figs. 1a–1d).

There was a multimodal distribution: for the Podolyanka cultivar, two clearly expressed maximum and two only apparent ones have been identified, which did not allow an approximation to the Gaussian distribution using different approximations [15]. The exposure effect significantly changed both distribution types. The swelling time declined from 7 to 5 h, the local maximum was combined, i.e., the distribution modality decreased. For the main part of the sample, the germination duration declined from 22 h (control) to 17 h (exposed) (Figs. 1a, 1b). Significant changes in the germination kinetics were observed in the Favoritka cultivar: the beginning of germination of the exposed samples was observed after 6 h instead of 12 h in the control; for the main part of the sample, the germination duration declined from 22 to 18 h (Figs. 1c, 1d). At the same time, in both cultivars, the percentage of "super-slow" germinating seeds, i.e., after 60 h of swelling, was decreased. This value decreased from 7–10% in the control to 1–2% under exposure. Changes in the germination kinetics accompanied changes in the DNA methylation profiles of FG- and SG-seedlings in control and exposed variants.

The electrophoregram of the nativity control of the isolated DNA is represented in Fig. 2. The data indicated absence of significant DNA fragmentation, potentially possible with chronic gamma exposure of dry seeds.

The electrophoregrams of the DNA amplification products' separation with both ISSR and RAPD-P6 primers showed the identity of the amplicon sets in all experimental variants (Figs. 3a, 3b), which indicates the absence of polymorphism in the corresponding sequences of the genome as well as hidden damage to exposed DNA, which can be detected during PCR.

The ISSR analysis data of MboI-restriction amplification products of Podolyanka cultivar (Fig. 4a, wells 1–4) indicated a difference in DNA methylation of control seedlings with low and high germination rate. A significant difference between the DNA methylation pattern of the control and exposed seedlings was observed for only a part of the exposed sample that germinated quickly (wells 3, 4). For the Favoritka cultivar, the difference in methylation pattern was observed between seedlings with different germination

rates for the control (wells 5, 7) as well as for exposed samples (wells 5, 6 and 7, 8).

The ISSR analysis of the amplification products of the MspI endonuclease restriction of the DNA Podolyanka seedlings (Fig. 4b, wells 1–4) indicated a difference in the methylation of fast- and slow-growing samples. During exposure, the difference between the methylation profile of control and exposed samples was observed only for a part of the sample with fast-to-germinate seeds (wells 3 and 4). For the Favoritka cultivar, no difference between DNA methylation control (tracks 5, 7) and exposed (tracks 6, 8) seedlings with different germination rates were observed.

A significant difference in RAPD-P6 amplification electrophoregrams of MboI endonuclease restriction (Fig. 5a, wells 1, 3) was observed in control groups of Podolyanka seedlings with different germination rates. Significant changes in the DNA methylation pattern during exposure of both groups were not detected (wells 2, 4). DNA methylation analysis of various Favoritka seedling groups of control variants detected significant differences in electrophoregrams (tracks 5, 7), while the differences in methylation pattern under exposure was only recorded for SG-seedlings (wells 5, 6).

The RAPD-P6 amplification results of MspI restriction digest run indicated differences in the amplicons electrophoretic spectra in the groups of fast- and slow-growing seedlings of the Podolyanka cultivar (Fig. 4b, wells 1, 3), which were grown under control conditions, and about the appearance of differences in the amplicons due to chronic gamma exposure only in SG-seedlings (tracks 1, 2).

DNA methylation pattern polymorphism of the Favoritka cultivar in FG and SG control seedlings was not detected (tracks 5, 7), but it was observed in the control and exposed groups of FG- seedlings (wells 7, 8).

Data about DNA methylation pattern (Figs. 4, 5) confirmed the results obtained earlier on the existence of DNA methylation polymorphism of seedlings with different germination rates [11–14], and they also indicated significant changes of the index under chronic gamma-radiation exposure. Thus, changes in the distribution character of the seed germination rate were associated with changes in methylation pattern in both fast- and slow-growing seed groups.

A quantitative evaluation of the DNA polymorphism degree of methylation pattern in fast- and slow-growing groups of plants exposed with chronic gamma-radiation was done.

According to modern concepts, epigenetic mechanisms combine DNA methylation, a number of chemical transformations of chromatin proteins, which causes changes in its conformation, and RNA interference. Since these processes are interrelated [19–22], their summarized characteristic can be changed in the DNA methylation profiles. Therefore, solving of the various problems could be detection of epigenetic polymorphism, which is based on estimation of simi-

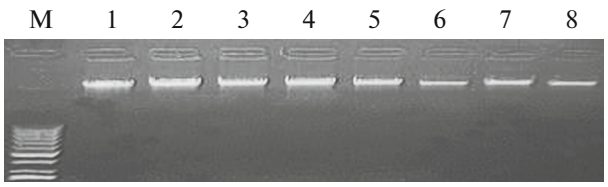

Fig. 2. Electrophoregram of isolated native DNA. Podolyanka (1–4) and Favoritka (5–8) cultivars: M—molecular marker GeneRuler 50 bp; 1, 5—SG-seedlings; 2, 6—SG-seedlings originated from gamma radiation-exposed seeds; 3, 7—FG-seedlings; 4, 8—FG-seedlings originated from gamma radiation-exposed seeds.

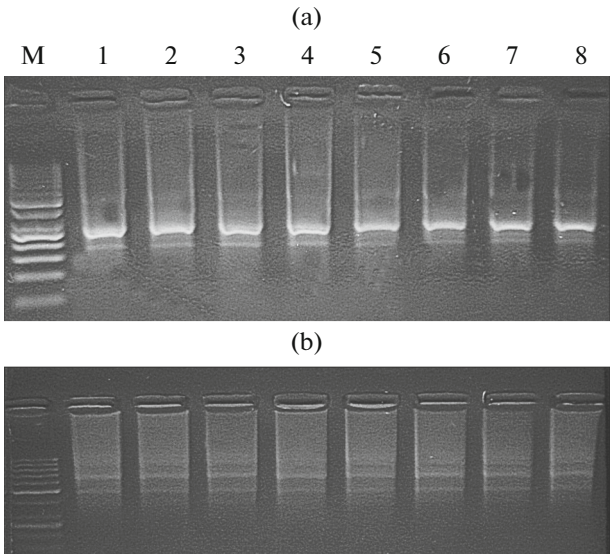

Fig. 3. Electrophoregram of amplification with (a) ISSR- and (b) RAPD-P6 primers. Podolyanka (1–4) and Favoritka (5–8) cultivars. See Fig. 2 for the remaining symbols.

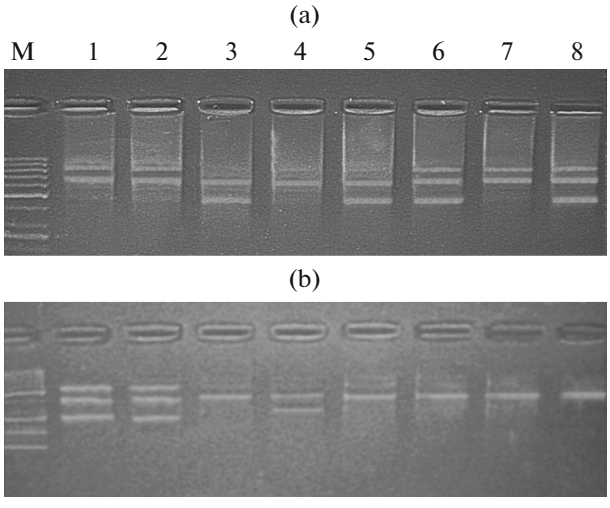

Fig. 4. Electroforegram of (a) MboI and (b) MspI restricts' ISSR amplification of Podolyanka (1–4) and Favoritka (5–8) cultivars. See Fig. 2 for the remaining symbols.

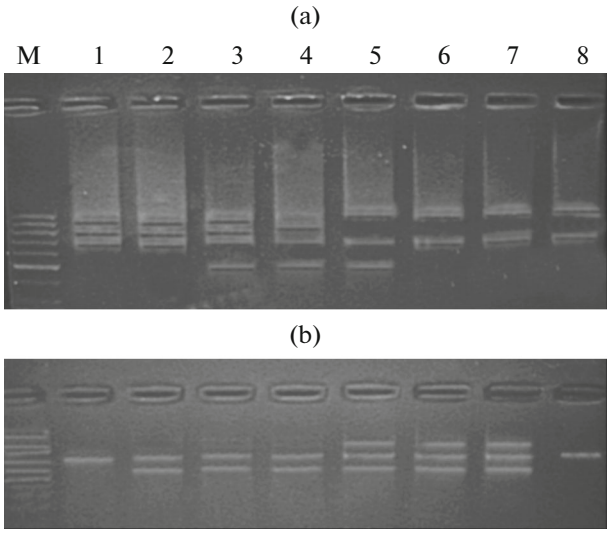

Fig. 5. Electrophoregram of (a) MboI and (b) MspI restricts' RAPD-amplification with primer P6 of Podolyanka (1–4) and Favoritka (5–8) cultivars. See Fig. 2 for the remaining symbols.

larity and differences in DNA methylation profiles [23, 24].

The differences in the epigenetic distances between the patterns of the DNA restriction products reflecting the DNA methylation profiles revealed in the present study indicate a decrease in the epigenetic distance between the DNA methylation profiles of fast- and slow-growing seedlings under exposure. Thus, the epigenetic distance calculated for the FG and SG seedlings of the Podolyanka cultivar was $D = 0.203$ under control conditions and this index decreased to $D = 0.062$ in the exposed seedlings. In the Favoritka cultivar under control conditions, the index was $D = 0.157$ and $D = 0.054$ in exposed seedlings.

Calculations of the changes in the epigenetic distance for both cultivars that have the highest ranges of the "ecological plasticity" category were conducted [14]. An increase in the seed germination rate during chronic exposure associated with a decrease in the epigenetic polymorphism level within the cultivar was indicated. It was mentioned that results obtained during the germination study of cultivated plants contradict with the results obtained earlier on the wild populations growing in the Chernobyl exclusion zone [25]. The environmental factors effect in the zone, including chronic-radiation exposure of 2.8–9.5 Gy dose range, led to a decrease in the germination rate and increase of the distribution in the seed sample, but the absolute values were unstable and varied non-monotonically over the years regardless of the accumulated dose.

In the population ecology, the concepts of life strategies are widely used [26, 27], one of the biological functions of which is the weakening of interspecific competition relationship. At the same time, natural mechanisms of weakening the effort of intraspecific competition are not actually considered. Ideas about diversity of environmental strategies are not applied to cultivated plant populations that have passed a long selection process and grow under artificial mono crop conditions. In enhancement in the mono crop, as a one-species population, competitive relationships are partially weakened by exogenous factors, primarily by agrotechnical influences (fertilization, irrigation, pest treatment). At the same time, natural mechanisms of reducing intraspecific (intracultivar) competition between organisms occupying one ecological niche are considerably interesting.

One of the reasons could be genetic polymorphism, which is to a varying degree present in any population (dropping) of cultivated plants. At the same time, according to the data of recent years, this indicator is comparatively low and considerably cedes to the epigenetic polymorphism index [23, 24]. This gives reason to assume that epigenetic polymorphism is an effective evolutionarily fixed factor of reducing interspecific competition relationship, including competitive relationships in mono crop. Confirmation to our assumption could be information on the wide distribution of this phenomenon in a variety of biological systems of both wild-growing [28] and cultivated plant populations [29] and differentiated animal tissues [30]. The prevalence of this phenomenon indicates that this is a general mechanism for increasing of the effectiveness of the functioning of biological communities at any organization level, aimed to reducing competitive relations and, possibly, strengthening cooperative societies. Thus, the obtained results indicate the possible causes of the negative influence of germination stimulation on the productivity of crop, already noted in the early studies of priming [4, 5], and also in the studies of hormesis and adaptive reactions associated with radiation exposure factors [31, 32].

It is known that, depending on the growth conditions, the plant organism redistributes its energy costs between productivity and the development of protective mechanisms [33]. Reduction of epigenetic polymorphism level during stimulation of germination can cause the emergence of two negative factors that reduce the crop productivity. First is to reduce the diversity of sustainability and adaptation mechanisms to negative environmental factors; second is to increase resource competition within the plant community, which also causes a decline in productivity.

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