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HORMESIS IN BARLEY (*Hordeum vulgare* L.) PLANTS DERIVED FROM γ-IRRADIATED SEEDS UNDER CONTRASTING WEATHER CONDITIONS

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Abstract

Identification of mechanisms of adaptive response to weak external exposure is one of the most complex and urgent problems of the modern biology. Such reactions include the effect of hormesis which is the stimulating effect of moderate doses of stressors (e.g. the low doses of various physical and chemical agents) repeatedly confirmed at all levels of the organization of living matter. The dynamics of the growth and development of barley (*Hordeum vulgare* L.) plants, grown from γ-irradiated barley seeds of Nur variety, which combines high productivity potential (up to 80 centner/ha), resistance to drought, good forage and brewing qualities of grain, high resistance to lodging and serious diseases, was studied in a field trial. It was shown that irradiation of seeds significantly influenced the development of plants throughout the vegetative period. The duration of the initial stages of ontogenesis was shortened, and the phase of full ripeness came on 5-7 days earlier than in the control. The length of the stems, the weight of 1000 grains, the number of grains per ear, the number of productive stems, the weight of straw and ears increased. The dependence of economically valuable traits on the dose of γ-irradiation of seeds was statistically significantly better described by models that take into account the effect of hormesis. The manifestation of the effect of pre-sowing γ-irradiation was different in the years with contrasting weather conditions. In the dry year of 2014, the increase in yield was determined by the increase in the number of productive stems, and under optimal conditions in 2015, this was due to the increase in the number of grains per ear. In 2016, an increase in the amount of precipitation by 2.5 times relative to the climatic norm leveled the stimulating effects. The results obtained in this study indicate that pre-sowing γ-irradiation of seeds notably affects the development of barley plants throughout the growing season, significantly changing the structure of the crop. In the plants from the seeds irradiated at stimulating doses, the manifestation of economically valuable traits was statistically significantly increased when vegetation seasons were contrasting in weather conditions. Realization of the effect of hormesis specifically depends on the conditions in which the plants developed.

Keywords: barley, gamma irradiation, seeds, hormesis, growth and development stimulation, yield

Identification of mechanisms of adaptive response to weak external exposure is one of the most complex and urgent problems of the modern biology. Such reactions include the effect of hormesis which is the stimulating effect of moderate doses of stressors existence of which was repeatedly confirmed at all levels of the organization of living matter for various physical and chemical agents [1-3[. The obtained experimental data in the last decades show that γ-irradiation of seeds in stimulating doses leads to a change in gene expression, quantitative and qualitative reconstruction of the enzyme systems [4, 5], changes in the concentrations of phytohormones [6], an increase in the mitotic index in root meristems [7, 8], which causes the growth acceleration and plant development in the early stages of ontogenesis. However, up to the present moment, there is no clear understanding of the mechanisms for the formation of stimulating effects. Moreover, in the field conditions, a number of factors influence the expression and the very possibility of hormesis manifestation [3, 9, 10], the role of which should be assessed to elucidate the mechanisms of response to low-dose irradiation and its practical use.

In our studies [11, 12], the response of barley seeds of different varieties to γ-irradiation at doses of 2-50 Gy was analyzed, and the range of γ-irradiation (10-20 Gy) was estimated in which stimulation of plant development in the early stages of ontogenesis occurs. It has been shown [4, 12] that the activity of a number of enzymes involved in metabolism and antioxidant defense in cells increases in the range of doses 16-20 Gy, stimulating the development of seedlings. Therefore, the arising question is whether the advantage obtained in the early stages of ontogenesis can be realized during the further plant development and crop formation. Keeping up this advantage by plants until the end of the growing season depends on many factors [9, 13]. In this, it is often not clear how short-term and prolonged stimulating effects of irradiation are formed.

The aim of this work was to evaluate the dynamics of growth and development of plants grown from γ-irradiated barley seeds and to clarify the role of growth conditions in the modification of these processes.

Techniques. Experiments were performed in 2014-2016 on spring barley (*Hordeum vulgare* L.) of Nur variety (1st reproduction). Barley seeds were subjected to pre-sowing irradiation using a γ-HPS 120 (60Co) device (Russia) at doses of 16-20 Gy previously established as having stimulation effect [11, 12], and also at doses of 8 and 50 Gy, the dose rate of 60 Gy/h. The moisture content of the seeds ($\approx$ 14 %) corresponded to GOST 12041-82 [13]. The dose of radiation was estimated using a DKS-101 dosimeter (Politekhform-M, Russia, rated relative measurement error 4 %).

The seeds were sown on the date of irradiation (8.05.2014, 15.05.2015 and 8.05.2016, the experimental field of the All-Russian Research Institute of Radiology and Agroecology). Plants from irradiated and control seeds grown on the same field on 20 plots measuring 2×3 m^2 were collected from the central part of each plot (1×2 m^2); the remaining area served as the first protective circuit. A border check rows of barley plants 50 cm wide (the second protective circuit) were planted along the perimeter of the whole test plot. The distance between the plots and from the border along the perimeter of the entire plot area was 40 cm. Plots on the experimental field in 2014 and 2016 were randomized, in 2015 set in an orderly manner. Four plots were used for each dose. Before sowing irradiated and test seeds, a fertilizer mixture was added in accordance with recommendations [10]: 4 kg per 225 m^2, N, P_2O_5, K_2O ratio of 1:1.15:1.45. Hydrolytic acidity, total exchangeable bases, exchangeable calcium and exchangeable magnesium were 4.92; 3.80; 2.87 and 0.52 mg-eq/100 g, respectively, humus — 1.63 %, mobile phosphorus and exchangeable potassium — 24.3 and 66.9 mg/kg, respectively; pH = 4.10. Irradiated and control seeds were sowed according to recommendations [10] in prepared rows with a 4-5 cm depth, located at a 5 cm distance from each other. Weeding was carried out when needed but at least once every 14 days. The yield was harvested at a stage of complete ripeness after 95-98, 103-106 and 99-100 days of growing, respectively, in 2014, 2015 and 2016. At least 400 plants were analyzed for each dose.

The onset of ontogenesis phases was determined by dividing the plot into 24 sections of 0.25 m^2. Ten plots were selected, on which the percentage of plants belonged to one or another stage of development was determined. The ontogenesis phase was considered to have occurred if it was manifested in no less than 75 % of the plants. After achieving complete ripeness, the plant were removed and following parameters evaluated: the height of the plants, the number of stems (tilling capacity), the average number of productive stems per plant, the number of grains per ear, the average straw weight of 100 plants, the average weight of 100 plant ears and 1000 seed weight. Straw, ears and seeds were weighted using an analytical balance OHAUS (USA). The parameters of the yield quality (proteins content, fiber, fat, dry matter and ash in grain and straw) were measured using an Infrapid-61 IR analyzer (Labor-MIM, Hungary). The weather condition data were obtained from the weather station (Obninsk, synoptic weather station index WMO ID 27606) [14].

Statistical processing was carried out in MS Excel, STATISTICA 6.0 (StatSoft Inc., USA), ORIGIN 6.0 (OriginLab Corp., USA), and R ver. 3.2.1 (R Foundation, USA) software. For the mathematical description of the results, the software environment R was used (Brain-Cousens and Cedergreen-Ritz-Streibig models, taking into account the possibility of hormesis manifestation) [15]. Samples were compared using the Mann-Whitney test. The differences were considered statistically significant at $p < 0.05$.

Results. Nur barley variety used in the study combines both high productivity potential (up to 80 centner/ha), resistance to drought, good forage and brewing qualities of grain, and high resistance to lodging and several dangerous diseases. In 2014, transit time of ontogeny phases in plants as dependent on the dose of pre-sowing γ-irradiation of seeds, was not studied. In 2015, the seedling phase was shorter in seeds irradiated with doses of 16 and 20 Gy (Table 1).

1. **Deviations in ontogenesis phases** (days) **as compared to control depending on the dose of γ-irradiation of barley (*Hordeum vulgare* L.) Nur variety seeds in the years with optimal and excessive moistening** (field plot trials, Kaluga Province)

Phase	2015					2016				
	control	8 Gy	16 Gy	20 Gy	50 Gy	control	8 Gy	16 Gy	20 Gy	50 Gy
Seedlings	8	0	–1	–2	–1	8	0	0	0	0
Tillering	15	–1	–1	–2	0	14	0	0	0	0
Stem elongation	15	0	0	+1	0	15	0	–2	–2	0
Heading	18	–1	0	+1	–1	17	0	0	0	0
Flowering	3	0	–1	–1	0	3	0	0	0	0
Milky ripeness	14	–1	–2	–1	0	12	0	0	0	0
Middle dough stage	15	0	0	–1	0	14	0	0	0	0
Complete ripeness	18	0	0	–2	0	17	0	0	0	0
Total, days	106	103	101	99	104	100	100	98	98	100

Apparently, the earlier appearance of complete shoots was caused by the acceleration of the root system development of plants grown from irradiated seeds, which we observed in our previous studies [4, 12]. It should be noted that the seedling phase was shorter in plants grown from seeds irradiated at a dose of 50 Gy, which does not belong to stimulants and does not improve morphophysiological indices in laboratory conditions [12]. The rapid passing the seedling phase in the plants grown from irradiated seeds determined the earlier onset of the tillering and stem elongation. However, the heading phase in all plants occurred almost simultaneously. By reducing the time of the flowering, milky, middle dough and complete ripeness in plants grown from seeds irradiated at a dose of 20 Gy, and the phases of flowering, milky, middle dough ripeness in plants from seeds irradiated at a dose of 16 Gy, complete ripeness occurred 7 and 5 days earlier, respectively, than in the control. Similar results [16] have been described in the literature, as well as a wave-like manifestation of the stimulating effect on ontogenesis [17, 18] when control plants at flowering reached the same phase of ontogenesis as the experimental ones but then again lagged behind till the phase of complete ripeness stage. In 2016, seed irradiation almost did not affect the time of passing the main phases of ontogenesis. Only earlier stem elongation was observed in plants from irradiated seeds, which led to a faster transition to tillering. However, this did not affect the general distribution of the ontogenesis stages in time. The lack of stimulation in passing ontogenesis phases in plants grown from irradiated seeds in 2016 was apparently associated with an extremely high amount of precipitation.

In 2014, the stem height in plants from seeds irradiated at 8 Gy statistically significantly exceeded the control (Fig. 1, A) and was characterized by the lowest variability of the studied parameter. In 2015, the height was statistically significantly higher throughout the entire dose range. In 2016, no increase in the height of productive stems compared to control was observed. A statistically significant increase in 1000 grain weight was detected in 2014 for 16 and 20 Gy and in 2015 for 20 Gy (see Fig. 1, B). In 2016, a statistically significant change in the 1000 grain weight was not found.

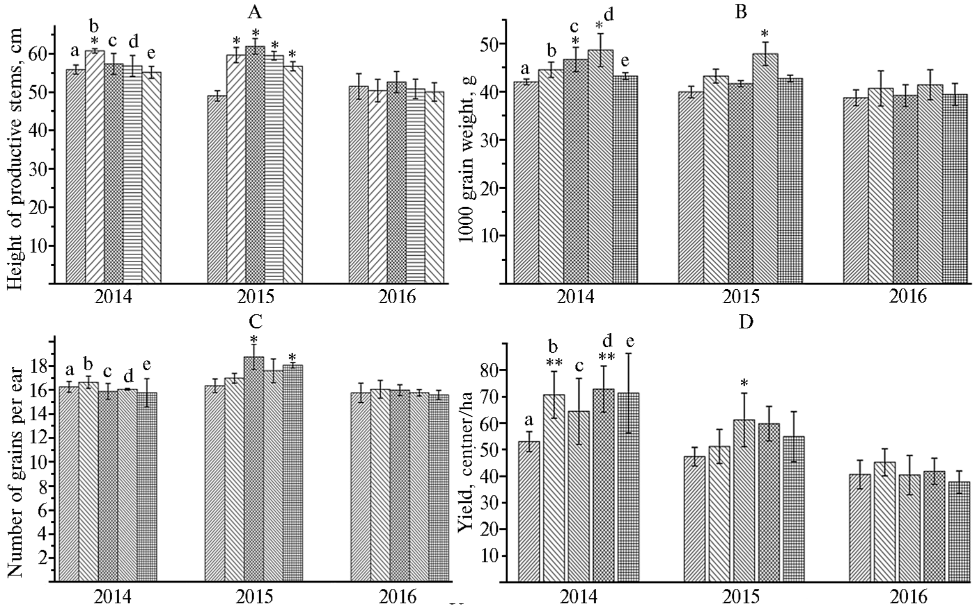

Fig. 1. Height of productive stems (A)**, 1000 grain weight** (B)**, the number of grains per ear** (C) **and the yield** (D) **depending on the dose of γ-irradiation of barley (*Hordeum vulgare* L.) Nur variety seeds in the years with precipitation deficit (2014), optimal conditions (2015) and an excess of moisture (2016):** a — control, b — 8 Gy, c — 16 Gy, d — 20 Gy, e — 50 Gy. The diagrams show the standard errors of the mean (field plot trials, Kaluga Province).
*, ** Differences with control are significant at $p < 0.05$ and $p < 0.15$, respectively.

Although the number of seed germs per ear is genetically controlled, the number of grains in the ear is strongly dependent on the interaction of the genotype and the environment [19]. Particularly strong influence on this element of the yield structure is provided by growing conditions in the zone of unstable moistening [20]. In 2014 and 2016, we found no statistically significant differences in the number of grains per ear, but in 2015 this value statistically significantly increased under the influence of doses of 16 and 50 Gy (see Fig. 1, C).

In 2014, the number of stems per plant increased statistically significantly for 16, 20 and 50 Gy (Fig. 2, A), and the number of stems with ear per plant was higher for 8, 20 and 50 Gy pre-sowing exposure of seeds. In 2015 and 2016, no statistically significant changes in the number of stems and stems with ears were detected. The ratio of productive shoots to the total shoots did not vary statistically significant for all the doses studied. Hence, the number of productive shoots increased or decreased proportionally to the total number of shoots. This is in line with the data that the ratio of productive stems to the total stem number is mostly constant for a species and does not depend on external factors [21, 22]. However, it is necessary to note the decrease in the ratio between the number of productive shoots and the total number of shoots in 2016 compared to 2014 and 2015.

In 2014, with an increase in the dose of seed irradiation, the weighs of ears and straw increased (see Fig. 2, B), but statistically significant differences were observed only for 8 Gy (straw) and 20 Gy (ears). In 2015, an increase in the ear weight was observed upon seed exposure to 16 Gy. The differences between the weight of straw and ears in test and control plants in 2016 were not statistically significant.

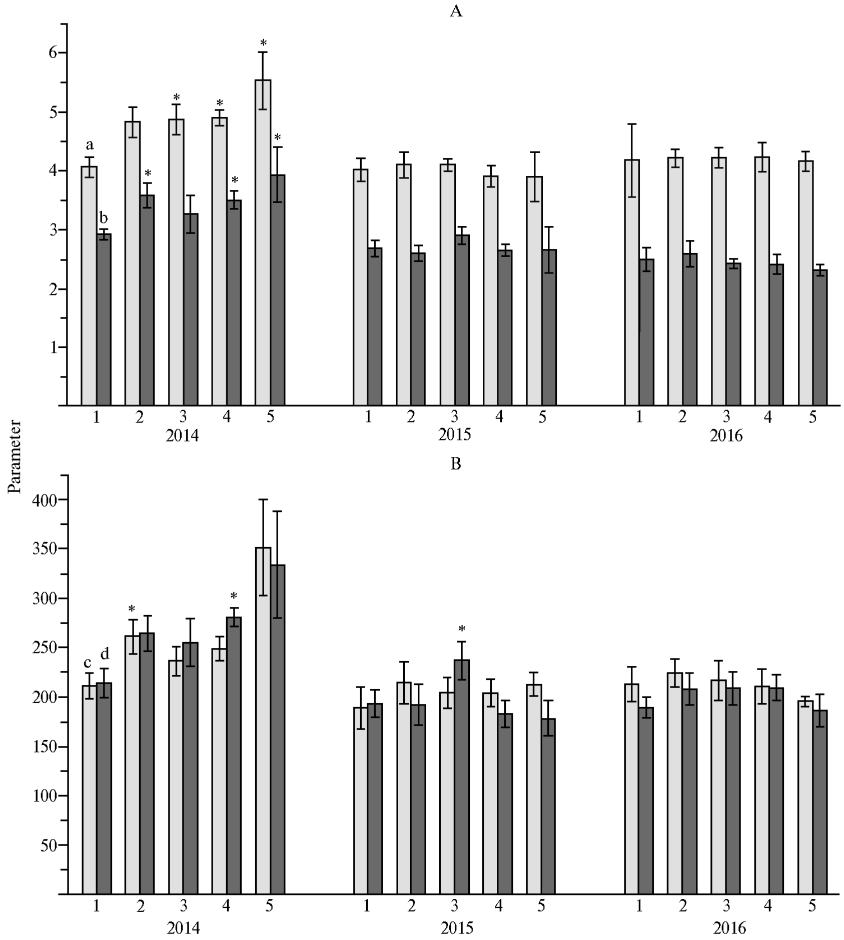

Fig. 2. Number (pcs.) **of stems** (a) **and stems with ears** (b), **and weight** (g) **of straw** (c) **and ears** (d) **depending on the dose of γ-irradiation of barley (*Hordeum vulgare* L.) Nur variety seeds in the years with precipitation deficit (2014), optimal conditions (2015) and an excess of moisture (2016):** 1 — control, 2 — 8 Gy, 3 — 16 Gy, 4 — 20 Gy, 5 — 50 Gy (field plot trials, Kaluga Province).

*, ** Differences with control are significant at $p < 0.05$; the diagrams indicate standard errors of the mean.

The obtained results made it possible to estimate the yield of barley (see Fig. 1, D). This indicator increased by 37, 34, 38 and 37 % in 2014, and by 8, 29, 26 and 19 % in 2015 for doses of 8, 16, 20 and 50 Gy, respectively. The yield increment in 2014 in 8 and 20 Gy variants, and also in 2015 with irradiation at 16 Gy was statistically significant ($p < 0.15$). The observed tendency to increase the yield indicates the positive influence of pre-sowing seed irradiation on the growth and development of derived plants. Apparently, the absence of a positive effect of pre-sowing γ-irradiation in 2016 was due to the excessive amount of precipitation (an almost 3-fold excess). The yield of barley in 2016 was about 40 centner/ha in the whole range of doses, which is due to a decrement in the parameters of the main elements of the crop structure (1000 seed weigh, grain number per ear and the number of productive stems) compared to those in 2014 and 2015 .

By influencing on metabolism, irradiation of seeds can lead to a change in the content of plant substances that determine quality of the products. Many researchers, in addition to the increment of the yield, noted an increase in sugar content of sugar beet, proteins in cereals, starch in potatoes, alkaloids in medicinal plants, vitamins in fruit and vegetable crops, carotenoids in carrots, ascorbic acid in cabbage, etc. [8, 16]. The biochemical analysis performed by us does not allow us to conclude that the composition of grain and straw has changed qualitatively in plants from irradiated seeds (all the studied indices were within the norm, data are not given).

The variability of weather conditions accounts for about a third of the variability in yield parameters in crops [23]. This confirms the comparison of the control values of the crop structure elements evaluated by us in the years different in weather conditions (Table 2). Therefore, weather conditions can significantly modify the effect of hormesis observed in the early stages of ontogenesis up to its complete elimination [8, 13, 23, 24].

2. Yield structure of barley (*Hordeum vulgare* L.) Nur variety plants derived from non-irradiated seeds (field plot trials, Kaluga Province)

Parameter	2014	2015	2016
Stem height, cm	55.88±1.17	49.03±1.35*	51.49±3.32
Weight of 1000 seeds, g	42.01±0.58	39.91±1.21	38.7±1.66*
Number of grains per ear, pcs.	16.24±0.45	16.34±0.57	15.57±0.81
Number of stems, pcs.	4.05±0.17	4.01±0.20	4.16±0.61
Number of stems with ears, pcs.	2.91±0.08	2.68±0.14	2.49±0.19*
Straw weight, g	214.18±14.76	193.01±13.98	189.3±10.30
Ear weight, g	211.49±13.15	188.89±21.39	213±17.60
Crop yield, centner/ha	50.01±3.77	47.34±3.52	40.56±5.40*

* Differences with the indexes recorded in 2014 are statistically significant at $p < 0.05$.

3. Weather conditions in the years of growing barley (*Hordeum vulgare* L.) Nur variety plants in the field plot trials (Kaluga Province)

Month	Sum of effective temperatures, °C			Precipitation, mm			Selyaninov's hydrothermal index		
	2014	2015	2016	2014	2015	2016	2014	2015	2016
May	423.3	347.7	339.6	19.1 (43)	70.2 (43)	117.3 (43)	0.45	2.01	3.45
June	468.7	511.6	512	78.9 (77)	80.0 (77)	268.4 (77)	0.99	1.56	5.24
July	612.6	545.8	612.7	59.0 (80)	106.7 (80)	282.7 (80)	1.04	1.95	4.61
August	302.7	470	294.9	8.2 (71)	50.0 (71)	94.0 (71)	0.91	1.06	3.18
Total	1808.2	1875.1	1759.2	165.2 (271)	306.9 (271)	762.4 (271)	0.85	1.63	4.33

Note. The norm of the sum of effective temperatures for barley in the Central Russia is 1200-1800 °C [24]; in parentheses, the norm of precipitation per month is indicated, mm [14]. Growing periods in 2014 — from May 8 to August 14, in 2015 — from May 15 to August 28, and in 2016 —from May 8 to August 15.

We compared the weather conditions of the growing seasons 2014-2016 and calculated the values of the Selyaninov's hydrothermal index (HTI) (Table 3) as $HTI = r/0,1\Sigma T_a$, where r is the sum of precipitation for a period with average daily temperatures above 10 °C, mm; ΣT_a is the sum of the effective temperatures during the growing season, °C [25]. The hydrothermal coefficient characterizes the agroclimatic conditions of cultivation [25]. The lower the HTI, the drier the growing period is. Extremely low precipitation along with the optimum sum of effective temperatures caused a very low HTI (0.45) in May 2014. Taking into account that the strongest influence of weather conditions on the results of pre-sowing seed irradiation manifests itself in the initial stages of ontogenesis [26], during insufficient moisture in May 2014, irradiated seeds gained an advantage in growth and development which affected the yield. In general, the whole growing period of 2014 (HTI = 0.85) is estimated as drought. Unlike in 2014, May 2015 was rainy (HTI = 2.01, which indicates an excessive moistening of the soil). The HTI value was also high for the entire observation period in 2015, but on the whole HTI was approaching the norm. Despite such different weather conditions in 2014 and 2015, the yield in experimental plants derived from irradiated seeds exceeded the control values for a number of important parameters (see Fig. 1, 2). The HTI for the growing season of 2016 reached an extremely high value of 4.33. This was the result of intense and abundant rains which 2.5 times exceeded the norm of precipitation for the central part of the Russian Federation and 4.5 times exceeded the values of 2014. Excessive precipitation together with a sufficient sum of effective temperatures leveled the stimulating effect of seed irradiation.

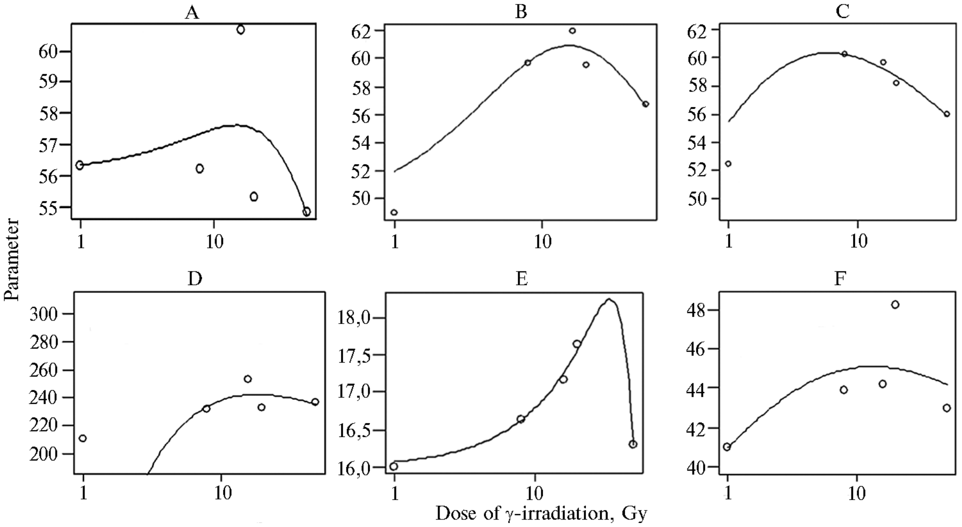

Fig. 3. Approximation of barley (*Hordeum vulgare* L.) Nur variety yielding parameters by Brain-Cousens and Cedergreen-Ritz-Streibig models taking into account the effect of hormesis (15): A — 1000 grain weight, g (2014, Brain-Cousens model, $p < 0.067$); B — stems height, cm (2015, Brain-Cousens model, $p < 0.098$); C — stems height, cm (2014-2015, Cedergreen-Ritz-Streibig model, $p < 0.013$); D — ear weight, g (2014-2015, Cedergreen-Ritz-Streibig model, $p < 0.011$); E — grain number per ear, pcs. (2014-2015, Cedergreen-Ritz-Streibig model, $p < 0.001$); F — 1000 grain weight, g (2014-2015, Cedergreen-Ritz-Streibig model, $p < 0.098$) (Kaluga Province, field plot trials; plants were grown from γ-irradiated seeds). For $p < 0.15$, the model describes the experimental data statistically significantly better than the logistic model.

In mathematical description of the obtained results (Fig. 3), it turned out that the response to irradiation in the range of stimulating doses by 1000 grain weight (see Fig. 3, A) and the stem height (see Fig. 3, B) corresponds to the Brain-Cousens model. As a matter of interest, even the combined data of field plot trials for two years with contrasting weather conditions, 2014 and 2015, for 1000 grain weight (see Fig. 3, F), stem height (see Fig. 3, C), ear weight (see Fig. 3, D) and the number of grains per ear (see Fig. 3, E) corresponded to the Cedergreen-Ritz-Streibig model. In all these cases, the effect of hormesis was statistically significant. For the remaining parameters, we did not found compliances to the Brain-Cousens and Cedergreen-Ritz-Streibi models (data not shown). It should be noted that in the present work the effect of pre-sowing seed irradiation was studied at the final stages of ontogenesis, when a number of factors actively influence the elements of crop structure. Nevertheless, the results of mathematical modeling (see Fig. 3) convincingly show that the advantage in the development of irradiated seeds in the early stages of ontogenesis can positively affect plant yielding and the yield structure in the field.

How does the obtained advantage at the onset of ontogenesis ensure an increase in the yields of barley? Formation of the plant root morphology and architecture occurs in the early stages of development and can vary greatly under the influence of external factors even within a single species [27]. In addition, in cereals the growth of the primary root system dominates during this period, and the quality of adventitious roots will determine development in the final stages of ontogenesis [28]. Thus, in drought conditions, barley plants, that have grown from irradiated seeds, due to a more developed root system in the early stages of ontogenesis have the advantage of obtaining water from the soil, which will eventually affect the subsequent stages of development. Therefore, it is not surprising that stimulation is manifested to the maximum extent in drought spring conditions, when rapidly growing seedlings were in more favorable conditions for nutrient and moisture supply [9, 16, 29] which was noted in 2014.

Despite the presence of other modifying influences, e.e. mineral deficit [9] and low soil temperature [16], the sum of effective temperatures and precipitation during the growing season remains as the key factors. Too dry or extremely humid conditions can minimize the stimulating effect of seed irradiation [16]. So, in the test of 2016 which was characterized by an excessive amount of precipitation during the entire growing season we did not record any significant changes in yields. However, weather conditions can influence the results of pre-sowing irradiation in a different way. In our experiments, the change in the water regime (2014-2015) did not lead to a leveling of the stimulating effect, but to its implementation by switching to an alternative course of ontogenesis, which ensured an increase in the yield under changed conditions. The “harvest triad” (the number of productive stems, the number of grains per ear and the 1000 grain weight), for the sake of complete realization, requires favorable conditions. Due to the self-regulation of these elements by agrocenosis under changing environmental conditions, the yield, when changing one parameter, can be maintained due to compensation by others [29]. Thus, in the drought (HTI = 0.85) 2014 year, in addition to the increment of the 1000 grain weigh, an increase in the number of productive stems was noted, and in the optimal 2015 year the yield gain was achieved due to the increased number of grains per ear. It should be noted that the control plants did not show wide variability of the studied parameters in contrasting weather conditions (the indices remained practically the same), except for the stems height in 2015, as well as the 1000 grain weight, the number of productive stems and the yield in 2016.

So, the present study indicates that pre-sowing γ-irradiation of seeds affects the development of barley plants throughout the growing season, substantially changing crop structure. Positive and statistically significant effects of stimulating doses on economically valuable traits were noted during cultivation in growing seasons with contrasting weather conditions. The realization of hormesis effect depends on the environmental factors in which plant development occurs.

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