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Research article

Radiosensitivity and mutability of wheat seed progeny cultivated under adverse environments

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A R T I C L E I N F O

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A B S T R A C T

This research analysed the growth process dynamics of soft wheat (*Triticum aestivum* L.) seeds cultivated in contrasting microclimatic conditions. We used acute gamma irradiation (5–50 Gy) as a provocative factor to detect hidden differences in the adaptive potential of seeds cultivated under adverse conditions (wet and cool field season) in comparison to seeds obtained under controlled conditions (hydroponic greenhouse). Seeds harvested from wheat plants cultivated in challenging field conditions demonstrated lower weight; moreover, their offspring also had a lower weight and seedling survival rate, as well as a delay in the formation of the fourth – sixth roots. The discrepancy in growth characteristics increased from the beginning to the end of the experiments and was particularly pronounced in offspring cultivated under adverse conditions throughout the entire experiment. The offspring of control seeds were more radioresistant than their field seed counterparts. At the same time, the "field" seeds were characterised by stimulation of growth and development of seedlings in their responses to irradiation. Few seedlings grown from "greenhouse" seeds exhibited evidence of root necrosis and twisted roots. Among the field plants, unusual developmental anomalies for 'greenhouse' seeds were encountered, including the disruption of gravitropism, thickening of roots, changes in the form of coleoptiles and leaves, and necrotic coleoptiles. Gamma irradiation stimulated an increase in the number of seedlings with various developmental disorders. In the case of seed progeny grown under adverse conditions, developmental anomalies were more frequent following irradiation relative to optimal conditions.

1. Introduction

Environmental factors (water, temperature, insolation, nutrients in the soil) are natural and necessary elements for the growth and development of plants, as well as for the successful maturation of seeds (Bewley et al., 2012). In response to fluctuations in weather conditions, living organisms demonstrate various biochemical and physiological mechanisms (Kolb and Robberecht, 1996; Hejnak et al., 2009; Martínez-Ballesta et al., 2009) in order to ensure their successful reproduction (Thakur et al., 2010).

Acute pre-sowing γ-irradiation of seeds is convenient to use for studying the genotype's reaction norm (Melki and Marouani, 2010; Jan et al., 2012; Ulyanenko and Oudalova, 2015; Preobrazhenskaya, 1971). This is due to the fact that radiosensitivity can be considered a manifestation of organisms' non-specific adaptation (Grodzinsky, 1989). The radiosensitivity of seeds is contingent on weather conditions during seed formation (Sparrow et al., 1971; Yanushkevich, 1964; Ul'yanenko et al., 2001). This may be associated with the interaction of various predictors, leading to synergism and in living organisms' responses to external influences (Sparrow et al., 1971; Petin et al., 1998; Pozolotina and Antonova, 2017). For example, the significant impact of weather conditions on the quality of the seed progeny of perennial herbaceous or woody species *Stellaria graminea* (Pozolotina et al., 2010), *Pinus sylvestris* (Geras'kin et al., 2015) and *Taraxacum officinale* (Pozolotina and Antonova, 2017) from natural populations is only manifested under conditions of chronic irradiation.

Therefore, the purpose of this study was to investigate the growth process dynamics and adaptive potential of *Triticum aestivum* L. seeds cultivated under contrasting microclimatic conditions. The study of this species is very important, since in annual plants reproductive efforts and energy budget are different from perennial plants (Primack, 1979; Pitelka, 1977). We hypothesised that wheat seeds grown in a cool and humid field environment would be characterised by reduced viability and radioresistance. We also expect that the synthesis of anthocyanins

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(natural antioxidants) will be stopped because the seedlings of the line that we have chosen for the experiments do not have a coloured coleoptile. This will lead to an increase in the number of seedlings with developmental anomalies, especially after acute pre-sowing γ-irradiation of 'field' seeds.

2. Materials and methods

2.1. Plant model

As a plant model, the line L140 (synonymous i:S29*pp-A1pp-D1pp3*) of soft wheat (*Triticum aestivum* L.) was used. The line was derived from the spring variety Saratovskaya 29. It was obtained in a previous study (Khlestkina et al., 2010) and described in detail elsewhere (Gordeeva et al., 2015). The seedlings of L140 have not anthocyanin pigmentation of coleoptile in norm.

2.2. Field site and weather conditions

In order to obtain seeds, wheat plants were cultivated in a greenhouse of Institute of Cytology and Genetics SB RAS (controlled conditions) and field facilities in the same year. Field conditions were extremely inauspicious during the summer (lower average daily t^{2009} = 10.6–18.5°C compared to 10-year average daily $t^{2005-2015}$ = 12.2–19.6°C; higher precipitation ΣP^{2009} = 222 mm·cm^{-1} (from 31 to 94 mm·cm^{-1}) compared to $\Sigma P^{2005-2015}$ = 206 mm·cm^{-1} (from 16 to 66 mm·cm^{-1}) according to "Ogurtsovo" weather station (54°54′N, 82°57′E).

2.3. Data sampling

2.3.1. Experimental design

The doses of acute irradiation were selected according to LD_{30} and LD_{50} in different wheat varieties described by (Preobrazhenskaya, 1971). The irradiation of air-dried seeds was undertaken on a γ-installation of the 'Igur-1' type with a source of ^{137}Cs (power of the source was 80 R·min^{-1}) immediately before sowing at doses of 0, 5, 10, 20 and 50 Gy. All seeds were disinfected with 1% $KMnO_4$ solution and plated in Petri dishes with a double filter moistened with distilled water. The experiment was conducted in 3 replicates. In each Petri dish, 25 seeds were sown, stacked according to the scheme from left to right 5 × 5 pieces. The location of each grain (seedling) remained unchanged throughout the experiment, thus enabling the seedlings' growth and development processes to be considered. In the experiment, 750 seeds were used and a total of 9,000 measurements were taken.

2.3.2. Seedling emergence rates and growth characteristics

Seed germination was synchronised for the first 24 h at 4 °C. The seed material was then germinated in the climate cell (Rubarth Apparate GmbH RUMED, Germany) at 20 °C under a 12-h light day. Petri dishes were randomised and pipetted daily with distilled water. On the fourth, fifth and sixth germination days, the length of first, second and third roots, the length of the coleoptile, the presence of fourth, fifth and sixth roots, leaves, various anomalies in the development of seedlings (changes in the shape of the roots and leaves and the appearance of necrotic formations in different organs) were measured in each seedling. The numbering of the roots is given as they appear (Fig. 1A). Seed germination was determined by the formula: $G, \% = \frac{N_1}{N_2} \times 100$, where N_1 – the number of germinated seeds, N_2 – the number of sown seeds. The survival of seedlings on days 4, 5 and 6 was calculated as follows: $S, \% = \frac{(N_1 - N_2)}{N_3} \times 100$, where N_1 – number of germinated seeds, N_2 – number of dead seedlings, N_3 – the number of sown seeds. The processes of leaf formation in seedlings were determined by $L, \% = \frac{N_1}{N_2} \times 100$, where N_1 – number of seedlings with leaves, N_2 – the number of sown seeds. The rate of growth processes (first, second and third roots and shoot length) was measured in each seedling (mm). The presence of fourth, fifth and sixth roots in seedlings was analysed in relative units to the number of sown seeds.

These criteria for assessing the quality of the seed progeny of wheat unexposed to acute irradiation (0 Gy) operated as the main indicators of viability (control). Radiosensitivity was determined by the criteria described above following pre-sowing seed irradiation at doses of 5–50 Gy. In the analysis of radiosensitivity, the absolute values were transformed to % to the corresponding unirradiated control. This helped clarify the effects of additional irradiation and facilitated comparison of the adaptive potential of seeds cultivated under different microclimatic conditions. Anomalies in the development of seedlings were estimated visually. They were calculated as: $A, \% = \frac{N_1}{N_2} \times 100$, where N_1 – the number of each anomaly in the Petri dish, N_2 – number of surviving seedlings. On the seventh day of the experiment the seedlings were weighed.

2.4. Data analysis

In order to test the statistical hypotheses, we used the asymptotic two-sided criterion for the difference between two proportions, the nonparametric Mann-Whitney test, ANOVA and MANOVA, the criteria for multiple Fisher comparisons (F), and the correlation analysis (R). An estimation of the growth dynamics of shoots and roots was carried out using canonical analysis. The normality of the distribution was verified using Kolmogorov-Smirnov criteria (d) with Liliefors and Shapiro-Wilks (W) corrections. The calculation was made using Statistica 10.0 (http://statistica.com/) and Past 2.11 software (Hammer et al., 2001).

3. Results

3.1. The weight of seeds and seedlings grown in contrasting conditions

The seeds from the greenhouse were healthy and heavy-eared, whereas under unfavourable field conditions a seed progeny of differing quality was matured, affected by fungi spores. The weight of 1,000 seeds grown in the field did not exceed 24.8–26.0 g, which was 61% of the weight of 'greenhouse' seeds (41.8–42.6 g). The differences were significant ($z = -2.06$, $p = 0.039$).

Similar data were obtained for the seedlings' weight. Without irradiation (Fig. 2), the average weight of one wheat seedling grown from 'field' seeds was significantly lower (36.8 mg) than a greenhouse counterpart (62.1 mg); $F_{1,4} = 43.48$; $p = 0.00274$. Following irradiation, the weight of the seedlings did not change with respect to corresponding unirradiated control (Fisher multiple comparisons, $p = 0.19$–0.61). However, in 'greenhouse' seeds with a maximum radiation dose, a 10–11% stimulation of the seedlings' weight was noted ($p = 0.00259$).

3.2. Viability of the wheat seed progeny grown under contrasting conditions

The 'greenhouse' seeds were characterised by high viability (Table 1). On the fourth day, seed germination reached its maximum and the survival rate of the seedlings remained consistently high throughout the experiment. By the sixth day, all seedlings had leaves. In comparison, almost all of the 'field' seeds' indicators were significantly lower. During the entire experiment, the rate of growth processes estimated along the length of 1–3 roots was similar under both optimal 'greenhouse' and extreme 'field' conditions, with the exception of third root on the fifth day of the experiment. However, among seedlings from 'field' seeds, the development of the fourth and fifth roots was delayed, and the sixth root was absent altogether. A similar advantage in the 'greenhouse' seeds was noted along the length of the largest leaf (in the initial days of the experiment this was along the length of the coleoptile).

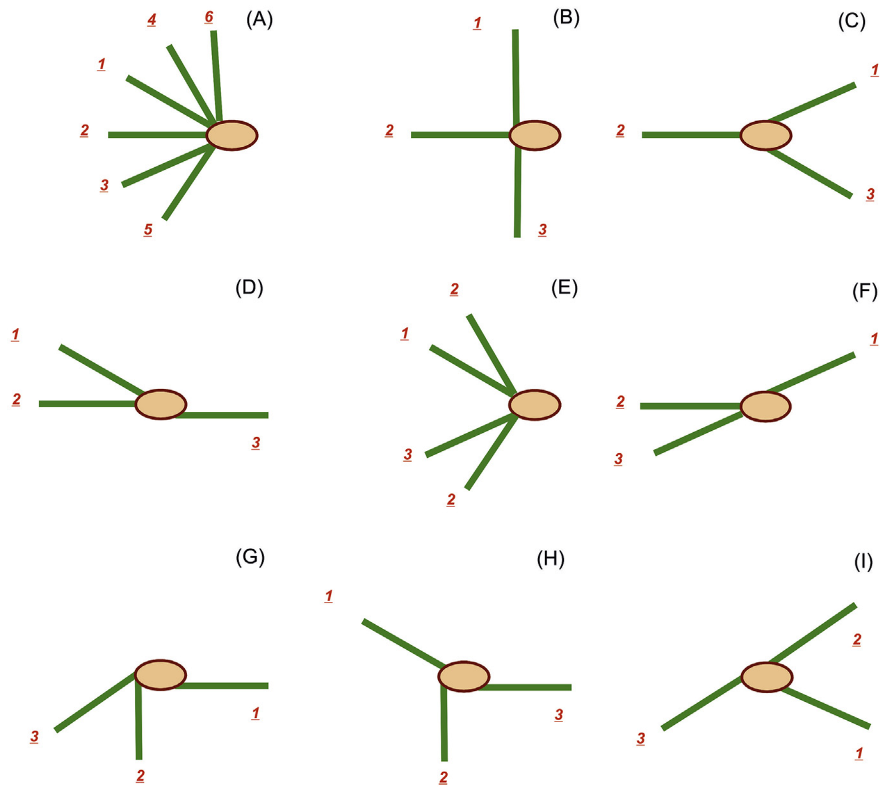

Fig. 1. Disturbance of the spatial arrangement of the wheat seedling roots of L140 line. Legend: A is the norm; B – root 1 and 3 sideways; C – root 1 and 3 back; D – root 3 back; E – root 2 sideways; F – root 1 back; G – root 1 back, root 2 sideways; H – root 2 sideways, root 3 back; I – roots 1 and 2 back.

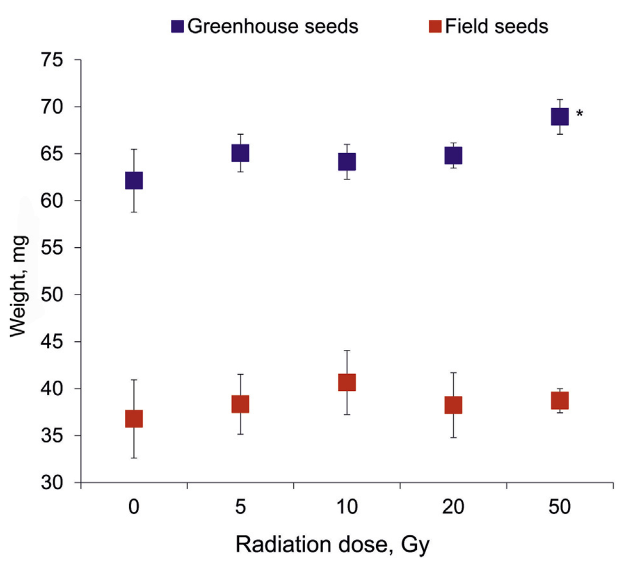

Fig. 2. Changes in the average weight of one seedling of line L140 after irradiation. * – difference between values for irradiated and intact (control) seeds are significant.

The results of the canonical analysis of the three-day dynamics of the growth of the shoots and the roots of the seedlings are shown in Fig. 3. Along the first canonical axis, which accounts for 86.2% of the intergroup variance, a discrepancy was observed between the lengths of the shoots, whereas along the second canonical axis (6.5% of the variance) this was between the roots' lengths. Thus, these parameters are characterised by allometry, i.e. the uneven growth of shoots and roots. All of the observed differences between the samples matured in contrasting conditions (according to the growth dynamics of shoots and roots) were statistically significant (Hotelling's p-values, Bonferroni corrected $p < < 0.002$), although the original growth characteristics (the fourth day of the experiment) were similar ($p = 0.11$).

With the growth of shoots and roots, the heterogeneity (variance) of features, which was especially pronounced in the 'field' seeds throughout the entire experiment, also increased. Thus, the ratio of shoots/second root was 0.58 in the 'greenhouse' seeds at the start of the experiment and 0.48 in the field experiments, and at the experiment end these figures were 1.17 and 1.26, respectively. This ratio in 'greenhouse' seeds changed by 145–202% from the third until the sixth day; the analogous alteration in the field was by 210–263%. In general, seeds cultivated in the field were characterised by less viability (seed germination, seedling survival, number of seedlings with leaves and the presence of fourth, fifth and sixth roots) and greater heterogeneity than those grown under optimal greenhouse conditions.

3.3. Radiosensitivity of the wheat seed progeny cultivated under contrasting conditions

Numerous studies of the radiobiology of cultivated and wild plants (Melki and Marouani, 2010; Sparrow et al., 1971; Pozolotina et al., 2010; Zaka et al., 2004; Popova et al., 1992) indicate that the reaction of plant seed progeny to acute gamma irradiation can be different. Effects depend, inter alia, on irradiation dose and the development stage of the organisms (Sidler et al., 2015). The suppression of growth processes and the death of seedlings, the stimulation of cell division and survival of seedlings, as well as an indifferent response when the indices do not differ from their own unirradiated control, are possible.

In the course of the entire experiment, for most of the indices the greenhouse seed offspring of wheat demonstrated high levels of radioresistance, with more than 84% of the responses to irradiation being indifferent at the experiment's end (Table 2). On the fourth to fifth days, the stimulation of root and leaf growth was observed (20–30% of responses), and was subsequently smoothed. At the same time, for 'field' seeds throughout the experiment, the predominance of

Table 1
The main indicators of the viability of seeds of the L140 wheat line grown under contrasting conditions (in the numerator X ± S.E, in the denominator - median (min-max)).

Condition	Day	Parameters									
		Proportion, %			Length, mm				Proportion, %		
		Germination	Survival	Number of seedlings with leaves	Shoot	Root 1	Root 2	Root 3	Root 4	Root 5	Root 6
'greenhouse' seeds	4	100.0	100.0	0.0	11.4 ± 0.7 11.6 (10.1–12.5)	16.6 ± 0.5 16.2 (15.9–17.6)	21.2 ± 0.8 21.1 (19.8–22.6)	16.9 ± 0.7 16.2 (16.0–18.6)	0.0	0.0	0.0
	5	100.0	100.0	21.3 ± 1.3 20.0 (20.0–24.0)	33.3 ± 0.46 32.9 (32.7–34.2)	32.9 ± 1.4 32.8 (30.6–35.4)	43.1 ± 2.1 39.0 (30.6–45.7)	35.7 ± 1.9 36.7 (32.0–38.2)	97.2 ± 1.32 96.0 (96–100)	94.8 ± 5.32 100.0 (84–100)	0.0
	6	100.0	100.0	100.0	53.8 ± 0.44 53.0 (52.4–53.9)	50.0 ± 2.1 49.8 (46.4–53.8)	58.2 ± 2.96 60.9 (52.3–61.5)	49.5 ± 1.9 50.2 (45.9–52.3)	100.0	100.0	14.8 ± 1.3 16.0 (12.0–16.0)
'field' seeds	4	96.0 ± 3.4 96.0 (92.0–100.0)	92.0 ± 2.3* 92.0 (88.0–96.0)	0.0	9.0 ± 0.6** 8.7 (8.2–10.0)	14.9 ± 1.1 14.5 (13.2–16.9)	23.4 ± 1.5 23.3 (20.9–26.0)	15.8 ± 1.4 14.9 (13.9–18.6)	0.0	0.0	0.0
	5	96.0 ± 3.4 96.0 (92.0–100.0)	92.0 ± 2.3* 92.0 (88.0–96.0)	16.0 ± 8.1 8.0 (8.0–32.0)	29.7 ± 1.5** 28.5 (28.0–32.7)	29.4 ± 3.5 27.9 (24.2–36.2)	40.4 ± 3.7 43.0 (33.0–45.2)	29.6 ± 2.9* 27.5 (26.2–35.3)	26.8 ± 1.76** 24.0 (16.0–40.0)	32.0 ± 1.15** 32.0 (24.0–40.0)	0.0
	6	96.0 ± 3.4 96.0 (92.0–100.0)	90.7 ± 2.7** 88.0 (88.0–96.0)	86.7 ± 4.8** 84.0 (80.0–96.0)	45.5 ± 1.8*** 44.3 (43.1–49.0)	43.7 ± 4.3 41.7 (37.3–51.9)	52.3 ± 3.9 55.1 (44.6–57.2)	43.2 ± 4.0 40.5 (38.0–51.0)	46.8 ± 1.85*** 42.0 (32.0–46.0)	46.8 ± 2.8*** 46.0 (24.0–60.0)	0.0

Note. Differences with control are significant: * – $p < 0.05$, ** – $p < 0.01$, *** – $p < 0.001$.

stimulation of not only growth processes but also the survival of seedlings (72–81% of all responses) was observed.

The results of the canonical analysis of the three-day growth dynamics of shoots and roots (Fig. 4) indicate that along the first canonical axis, which accounts for 85.9–88.8% of the intergroup variance at different doses, differences emerged between the shoot lengths (and the third root at a dose of 20 Gy). Along the second canonical axis (4.9–8.1% variance), the differences were between the root lengths. Thus, akin to the case without acute irradiation, these parameters are characterised by allometry with a predominant growth of the second root. All of the differences observed between the post-irradiation growth dynamics of the shoot and roots for the wheat seed progeny matured under contrasting conditions were statistically significant (Hotelling's p-values, Bonferroni corrected $p < < 0.0098$), aside from the fourth day of the experiment (50 Gy, $p = 0.1537$). Irradiation proved to constitute an additional factor that increases the variance of features, especially in 'field' seeds. The ratio of shoot/second root ranged from 0.54 to 0.70 (third day), 0.93–1.25 (fourth day) and 1.05–1.22 (fifth day). This was more stable in 'greenhouse' seeds irrespective of irradiation dose: 0.66–0.73 (third day), 0.98–1.09 (fourth day), 1.17–1.20 (fifth day). High irradiation doses caused a similar change in the shoot/second root ratio, equal to 1.31–1.32, for all seeds.

Thus, the wheat line of L140 was characterised by significant resistance to acute gamma irradiation. However, for seeds grown in the field, considerable heterogeneity in responses to irradiation could be observed, characterising both the stimulation of the growth and the development of the seedlings, and the delay in the development of the seedlings compared to the 'greenhouse' seeds.

3.4. Mutability of the wheat seed progeny cultivated under contrasting weather conditions

Most anomalies in the seedlings' development of the L140 line proved to be associated with various root changes. Several disorders were regularly observed in the same seedling. Throughout the entire experiment, the seeds cultivated under greenhouse conditions rarely formed seedlings with root necrosis and twisted roots (1.3–2.7% of survivors). In contrast, these indices were higher in the 'field' seeds (1.5–29%). In addition, in the sample matured in the field, the following anomalies of seedlings were observed: a violation of geotropism (1.4%), a thickening of the roots (1.5–8.7%), a change in the form of coleoptile (12.6%) and leaves (9.9%), necrotic coleoptile (1.5%) and the violation of the spatial arrangement of the roots (4.4–30%, see Fig. 1).

Provocative irradiation increased the proportion of seedlings with various developmental disorders. Dose-response relationships were nonlinear (S-shaped curve) in the both seed cases. In the case of 'greenhouse' seeds, the maximum number of morphoses was observed from a dose 20 Gy. In the 'field' seeds, the maximum number of morphoses appeared after irradiation from dose 10 Gy. It means that the quasi-threshold dose, which assesses the ability of cells to repair and characterizes the S-shaped curve arm length, was lower for 'field' seeds than for 'greenhouse' seeds. At the same time, the proportion of seedlings with anomalies in the 'field' seedlings of wheat was higher ($z = 2.82$, $p = 0.421$) than that of the 'greenhouse' seeds (Fig. 5).

In 'greenhouse' seeds, after pre-sowing irradiation, no anthocyanin pigmentation of the coleoptiles or neoplasms (tumour-like outgrowths) were detected. Coleoptile shape changes occurred sporadically in 1.33% of 'greenhouse' seedlings at a dose of 10 and 20 Gy. At once following the pre-sowing irradiation of the 'field' seeds, anthocyanin pigmentation of the coleoptiles was found at doses of 20 and 50 Gy (Fig. 6). This indicator was positively correlated with the appearance of neoplasms in seedlings ($r = 0.92$, $p = 0.000001$) and changes in the form of the coleoptiles ($r = 0.74$, $p = 0.0017$). The appearance of tumours can be associated with the uncontrolled growth of cells after irradiation. All indicators, except for changes in the coleoptile form

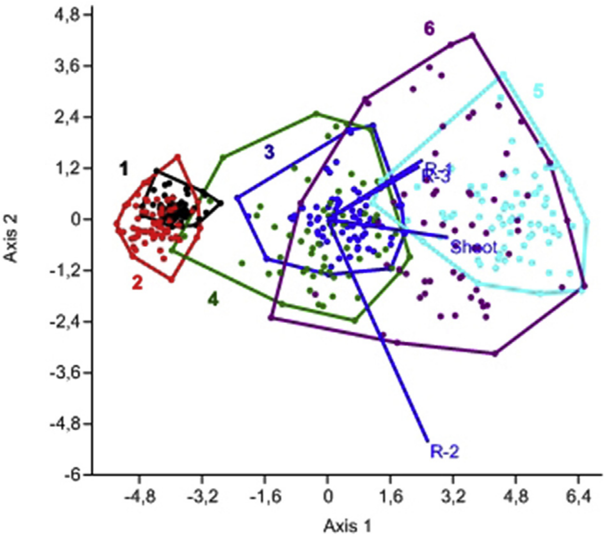

Fig. 3. Distribution of seedling growth parameters of line L140 in the dimension of the first canonical variables. Legend: *1* – greenhouse, day 4; *2* – field, day 4; *3* – greenhouse, day 5; *4* – field, day 5; *5* – greenhouse, day 6; *6* – field, day 6; R – roots.

(linear response), were characterised by S-shaped curves, with the quasi-threshold dose for anthocyanin pigmentation and for neoplasms of the coleoptiles being equal. In addition, seed irradiation resulted in the formation of a seedling anomaly that we label "*dancer*" (the frequency of occurrence was 1.4–11.6%). Such seedlings were characterised by multiple disorders, including twisting and thickening of the roots as well as a change in their spatial arrangement (the seedlings rose above the surface).

4. Discussion

Environmental factors (such as water, temperature, insolation, nutrients in the soil) are natural and necessary elements for the growth and development of plants, as well as for the successful formation and maturation of seeds (Bewley et al., 2012). A lack or excess of any element causes the conditions necessary for the growth of plants to shift away from the optimum zone, triggering various molecular, biochemical and physiological mechanisms that support homeostasis, including the synthesis of microRNA, the expression of MYB genes, NAC, WRKY, DREB transcription factors, enzymes CAT, APX, GR and lipid content (Pareek et al., 2009; Gill and Tuteja, 2010). These processes regulate changes in plant morphogenesis (Yang et al., 2013).

The adverse conditions during the seed formation of the line L140 (low temperature and excess precipitation in the field) stimulated the reduced weight of 1,000 seeds, the diminished weight and survival of seedlings, and delays in the formation of the fourth to sixth roots. One of the reasons behind the inhibition of root growth could comprise a change in the mechanical properties of the cytoderms, resulting from the disorganisation of cortical microtubules under stress conditions (Ktitorova et al., 2012).

For the shoots and roots of seedlings grown under different conditions, allometry was typical. The variance of growth characteristics increased from the beginning to the end of the experiments and was particularly pronounced in offspring cultivated under difficult conditions throughout the entire experiment. On the one hand, some authors (Arredondo and Johnson, 2011) consider the allometry of organs (in particular roots) an adaptive feature, because it enables them to compete for soil nutrition. On the other hand, symmetry provides the body with an effective means of overcoming physical limitations and studying three-dimensional space (Damerval et al., 2017).

The radiosensitivity of seeds is also contingent on weather conditions during their formation (Sparrow et al., 1971). It was shown that more radiosensitive seeds are formed under conditions of high humidity and low temperature (Yanushkevich, 1964). Strengthening the damaging effect of radiation in difficult weather conditions has been demonstrated by other authors (Ulyanenko and Oudalova, 2015; Ul'yanenko et al., 2001; Pozolotina and Antonova, 2017). The radioresistance of the seed progeny of greenhouse wheat (control conditions) was high in most indices. Indifferent responses to irradiation predominated, and stimulants were less common. At the same time, the 'field' seeds were characterised by the stimulation of the growth and development of seedlings in their responses to pre-sowing gamma radiation. This appears to be associated with the initial quality of seed progeny, because high-quality seeds work at the limit of their possibilities, and so they do not respond to irradiation with stimulation. In contrast, for seeds of medium quality, a reaction was typical (Kuzin, 1995). In general, the L140 wheat line has a high level of resistance to gamma irradiation, consistent with data regarding the significant radioresistance of the variety Saratovskaya 29 (Ul'yanenko et al., 2001; Korneev et al., 1985), on the basis of which the line L140 was generated.

Table 2
Radiosensitivity of seeds of the L140 wheat line grown under contrasting conditions (5–50 Gy).

Condition	Day	Parameters								Totally, %		
		Proportion, %		Length, mm				Proportion, %		0	+	–
		Survival	Number of seedlings with leaves	Shoot	Root 1	Root 2	Root 3	Root 4	Root 5			
'greenhouse' seeds	4	0000	no	-+0+	-0-0	000+	−00+	no	no	12 ***60.0***	4 20.0	4 20.0
	5	0000	-+++	0+++	0++0	0000	0000	0000	0+0+	21 ***65.6***	10 31.3	1 3.1
	6	0000	0000	0+++	−000	000-	0000	0000	0000	27 ***84.4***	3 9.4	2 6.3
'field' seeds	4	00+0	no	0+++	+++0	++++	++++	no	no	5 25.0	15 ***75.0***	0 0.0
	5	00++	++++	0+0+	++++	++++	++++	++++	++-0	5 15.6	26 ***81.3***	1 3.1
	6	00++	00++	0+++	++++	++++	++0+	0++-	+++0	8 25.0	23 ***71.9***	1 3.1

Note: "0″ does not differ from its own unirradiated control; "+" is stimulating effect (more than 105% of non-irradiated control taken as 100%); "-" is suppressing effect (less than 95% of the unirradiated control). Each symbol in the cell corresponds with the dose irradiation. In the column "Totally", the numerator denotes the quantity and the denominator shows the proportion of effects in the total reaction pool following acute irradiation.

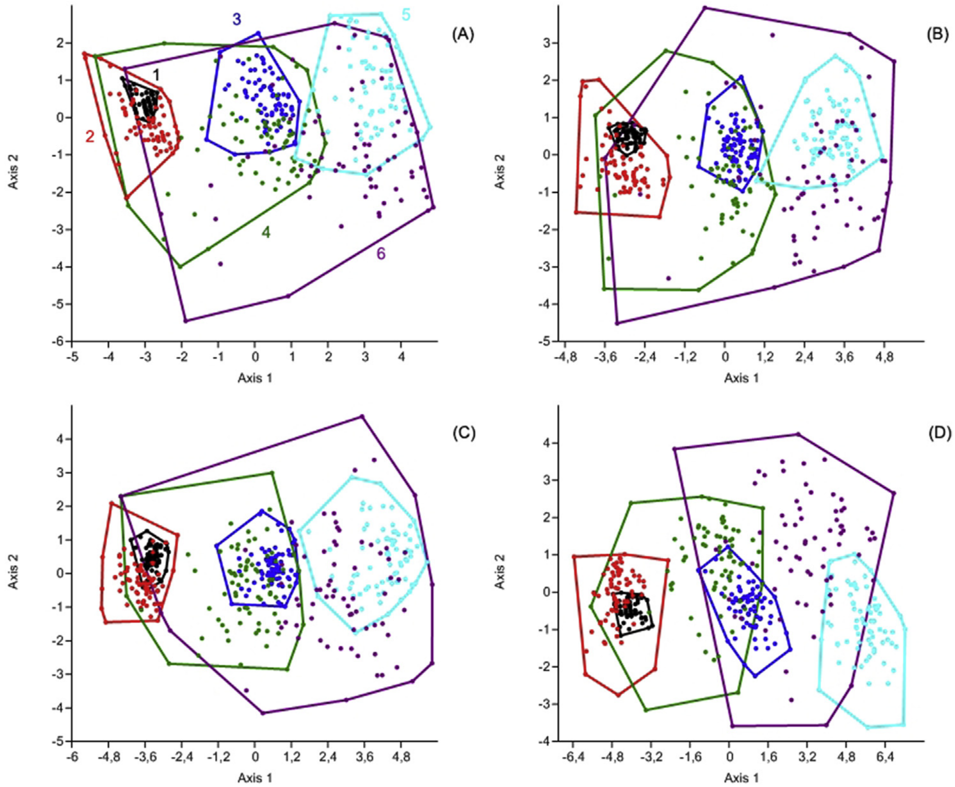

Fig. 4. Distribution of growth seedling parameters of line L140 in the dimension of the first canonical variables. Legend: A – 5 Gy; B – 10 Gy; C – 20 Gy; D – 50 Gy; *1* – greenhouse, day 4; *2* – field, day 4; *3* – greenhouse, day 5; *4* – field, day 5; *5* – greenhouse, day 6; *6* – field, day 6.

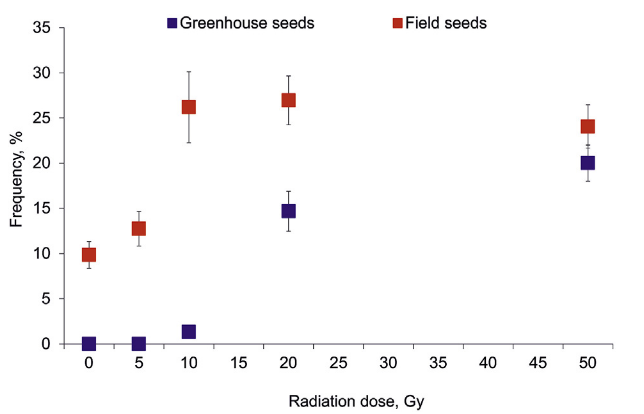

Fig. 5. Occurrence frequency of the wheat seedlings of L140 line with anomaly "change in leaf shape" at the experiment's end.

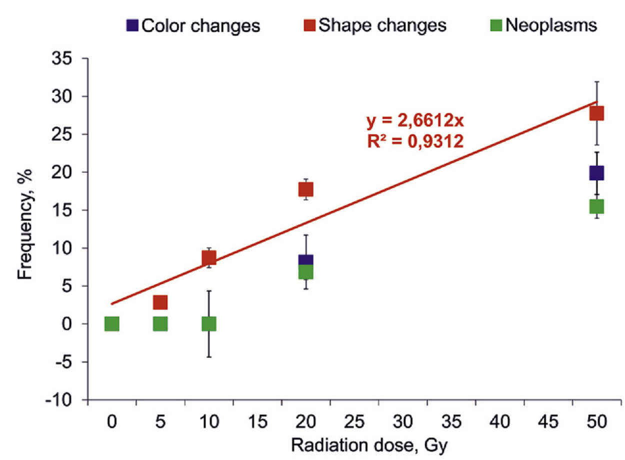

Fig. 6. Frequency of occurrence of wheat seedlings of L140 line with coleoptile anomalies at the experiment's end.

In the course of the experiment, the majority of anomalies in L140 wheat seedlings were manifested in various root changes. Seedlings with root necrosis and twisted roots were rarely formed from the 'greenhouse' seeds. In the field seed offspring, developmental anomalies that were unusual in the case of greenhouse seedlings were encountered, including the disruption of geotropism (gravitropism), thickening of the roots, changes in the form of coleoptiles and leaves, and necrotic coleoptiles. It must be acknowledged that leading role in the regulation of root gravitropism is played by auxin and active forms of oxygen (Joo et al., 2001). In a previous study (Ktitorova et al., 2006), the thickening of the roots was explained by the cessation of the division of rhizoderm cells and the outer layers of the cortex in a meristem, subsequent vacuolisation, and as a consequence the radial expansion of cells.

Some environmental factors, especially ionising radiation, are strong mutagens (Pozolotina and Antonova, 2017; Frolova et al., 1993; Oudalova et al., 2002; Yoschenko et al., 2016). In our experiments, the proportion of seedlings with various developmental disorders grew nonlinearly following gamma irradiation, and the mutability of seed progeny cultivated under adverse field conditions was significantly higher than in the case of the offspring of control 'greenhouse' seeds. The fragmentary pigmentation of coleoptiles in the field plants (normal line L140 is not marked in colour) was likely to have constituted a response to oxidative stress. It is known that the synthesis of anthocyanin pigments, which are natural antioxidants, is activated or amplified in response to unfavourable environmental conditions (Gordeeva et al., 2018). The appearance of outgrowths (tumour-like protrusions) in seedlings may be caused by a stimulating effect after irradiation, as well as by a violation of the regulation of cell division relative to the plane of the layer. Considering the fact that tumour-like protrusions were only apparent in seedlings grown from 'field' seeds (unfavourable conditions), we should not exclude the contribution of phytopathogens developing on germinating 'field' seeds in this process (Skibbe et al., 2010).

5. Conclusions

Following acute gamma irradiation, we have revealed a wide range of pronounced differences characterising the increased radiosensitivity and mutability of the seed progeny of wheat cultivated under adverse environment relative to seed progeny obtained under optimal (greenhouse) conditions.

Contributions

E.V.A. and E.K.K. conceived the project. E.K.K. had collected the field and greenhouse materials. E.V.A. and E.K.K. designed the experiment and conducted all measurements. E.V.A. conducted the statistical analysis and figure design. E.V.A. wrote the first draft of the manuscript and interpreted the biological results. All authors finalized the manuscript.

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