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DROUGHT TOLERANCE OF WHEAT *Triticum aestivum* L. PLANTS DIFFERING IN THE DROUGHT ADAPTATION STRATEGIES DURING EARLY ONTOGENESIS

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Abstract

The early stages of ontogenesis during which plants are most sensitive to water deficit, is one of the most crucial in the plant development. Soft wheat (*Triticum aestivum* L.) is one of the most widespread valuable crops in the world and in the Russian Federation. In the course of natural and artificial selection on the territory of Russia, two ecological groups of wheat were formed, the West Siberian forest-steppe and the Volga steppe ecotypes which differ significantly in the strategy of adaptation to drought. The spring drought is typical for Western Siberia, and, therefore, wheat plants of the forest-steppe West Siberian ecotype grow slowly at the initial stage of ontogenesis. In the south-eastern regions of the European Russia, in particular, in the Volga region, drought occurs later, and cultivars of the steppe Volga ecotype, on the contrary, grow intensively at the beginning of the growing season in order to develop an extensive root network by the time of the onset of summer drought. This work has revealed for the first time the role of drought-induced changes in the hormonal balance and in the content of the amino acid proline on the degree of drought tolerance of wheat ecotypes that differ in their adaptation strategy to drought at the initial stage of ontogenesis. The goal of the work was to evaluate various physiological and biochemical parameters of wheat plants of Zauralskaya Zhemchuzhina (forest-steppe West Siberian ecotype) and Ekada 70 (steppe Volga ecotype) cultivars during early ontogenesis under normal and drought conditions. In the first series of experiments, seeds were germinated in Petri dishes (15 seeds per dish) on filter paper moistened with 5 ml of 4 %, 8 % and 12 % sucrose solutions to simulate drought. Petri dishes were placed in a climate chamber and the seeds were germinated in the dark at 22 °C for 3 days. Seeds germinated in distilled water served as a control. On day 3, the energy of seed germination was calculated as the ratio (%) of the number of germinated seeds to the total number of seeds used. The length of the main root of the seedlings was measured. In the second series of tests, pot experiments were carried out under controlled conditions. Seeds were sown in 15 liter pots (30 plants per pot, sowing depth was 4-5 cm, distance between rows was 2.5 cm, and distance between plants in a row was 2.5 cm). In the control pots, the soil moisture was maintained at 70 % of the total water retention capacity of soil. Other plants were subjected to early soil drought by not watering until the soil moisture dropped to 30 % of the total water retention capacity of soil. On days 7, 8 and 9, the fresh and dry weight of control and drought-stressed seedlings were measured. The contents of cytokinins (CK), indoleacetic acid (IAA) and abscisic acid (ABA) in 10 seedlings with fresh weight of 0.9-1.0 g on day 7, 8 and 9 were determined by the enzyme-linked immunosorbent assay (ELISA) using hormone specific rabbit antibodies and peroxidase-labeled anti-rabbit antibodies. Extraction of free proline and its quantification were also carried out. It was revealed that concentrated solutions of sucrose simulating drought reduced the energy of seed germination and inhibited the main root growth of 3-day-old seedlings of both wheat ecotypes. It should be noted that the inhibition of both seed germination and main root growth was more pronounced in the Zauralskaya

Zhemchuzhina cultivar. Soil drought also suppressed the growth of 7-9-day-old seedlings, and the suppression was also more pronounced in the Zauralskaya Zhemchuzhina plants. We revealed an imbalance in phytohormone levels in 7-9-day-old seedlings of both cultivars associated with the drought-induced accumulation of ABA and a decrease in the contents of CK and especially auxins. However, in Ekada 70 seedlings the range of drought-induced changes in hormonal balance was noticeably smaller compared to Zauralskaya Zhemchuzhina plants. It was also found that the soil drought led to an increase in the content of proline, an important osmoprotectant, while a higher concentration of proline was characteristic of 7-9-day-old seedlings of Ekada 70 cultivar both under normal and stress conditions. To summarize, our findings indicate a higher drought tolerance during early ontogenesis of the steppe Volga ecotype plants compared to the forest-steppe West Siberian ecotype plants. This is probably due to less altered phytohormone profiles and the increased osmoprotectant proline accumulation in the steppe Volga ecotype plants under drought.

Keywords: *Triticum aestivum*, wheat, ecotypes, drought, hormonal system, proline

Drought is one of the most common stresses that results in disruption of metabolism and significant crop yield loss, including wheat [1-3]. Early ontogenesis when plants are especially sesusceptible to unfavorable factors is crucial for wheat development. Moisture deficiency causes a decrease in seed germination, inhibition of seedling emergence and growth, a lag in crop growth, which, in turn, leads to a significant decrease in yield [4, 5]. Therefore, early drought resistance is of particular interest in order to identify the most effective mechanisms of plant protection and crop management under unfovorable water regime [5-7].

During natural and artificial selection under various drought conditions, two groups of wheat significantly different in adaptation strategy appeared, the forest-steppe West Siberian ecotype and steppe Volga ecotype [8-10)]. Distinquishing features of the West Siberian ecotype plants are slow germination and a rather long tillering stage due to the spring drought characteristic of the Western Siberia regions. Plants of this ecotype use abundant summer rains typical of the Western Siberian climate zone for rapid growth and development. Varieties of the steppe Volga ecotype intensively grow in spring using the soil moisture reserves, therefore, by the time of summer drought, the plants form an extensive network of roots providing a good harvest. That is, differences in adaptation to drought in wheat varieties of the forest-steppe West Siberian and steppe Volga ecotypes are especially pronounced at early plant development. Therefore, studying the features of early protective mechanisms of these ecotypes during moisture deficiency will allow progress in understanding the mechanisms of their drought resistance.

In this work, drought-induced changes in the hormonal balance and the content of the amino acid proline were revealed for the first time in the forest-steppe West Siberian and steppe Volga ecotypes of wheat at the initial stage of ontogenesis. Seedlings of the steppe Volga ecotype showed more pronounced resistance to dehydration icompared to plants of the forest-steppe West Siberian ecotype, which is due to significantly lower amplitude of stress-induced rearrangements in the content of phytohormones and higher accumulation of proline.

The purpose of the work was to assess the physiological and biochemical parameters of wheat plants of the varieties Zauralskaya Zhemchuzhina (forest-steppe West Siberian ecotype) and Ekada 70 (steppe Volga ecotype) in the initial stage of their ontogenesis under normal and drought conditions.

Materials and methods. Seeds of soft spring wheat (*Triticum aestivum* L.) varieties Ekada 70 (the steppe Volga ecotype) and Zauralskaya Zhemchuzhina (forest-steppe West Siberian ecotype) provided by the Chishminsky breeding center of the Bashkir Research Institute of Agriculture (Republic of Bashkortostan, Chishmy) were pre-sterilized with 96% ethanol and used in two experiments.

In the first experiment, 15 seeds per Petri dish were laid out on filter paper moistened with 5 ml of 4%, 8% and 12% sucrose solutions to simulate drought [11, 12]. The Petri dishes were placed in a TSO-1/80 SPU thermostat (JSC Smolensk

Special Design and Technology Bureau of Programmed Control Systems, Russia) and the seeds were germinated in the dark at 22 °C for 3 days. Control seeds were germinated in distilled water. On day 3, the germination energy was calculated by the ratio (%) of the sprouted seeds to the total number of seeds intended for germination. Seeds that produced a root of minimal length were considered germinated. In sprouted seeds, the length of the main root was measured [13].

In the second experimetn, pot trials were carried out under controlled conditions. Seeds were sown in 25×25×25 cm/15 l container, sowing depth of 4-5 cm, distance between rows 2.5 cm, distance between plants in a row 2.5 cm, 30 plants per container. Agrotechnical expanded clay (2-3 cm layer, Terra Master LLC, Krasnoyarsk) was placed at the bottom of each container. Soil with an optimal NPK ratio (pH 6.5, humidity 65%; Veltorf LLC, Russia) was poured on top of the expanded clay. Plants were grown at 21-23 °C, 16-hour photoperiod, illumination of 360 $\mu mol \cdot m^{-2} \cdot s^{-1}$, and 60% air humidity. Some plants were subjected to early soil drought. During its modeling, watering was not carried out until the moisture content reached 30% of the soil's total moisture capacity (TMC). In the control, humidity was maintained at 70% of the TMC.

Physiological and biochemical parameters were assessed at the germination stage on 7-9-day old seedlings. The stages of ontogenesis were as proposed for cereals by T.B. Batygina [14]. On days 7, 8 and 9 of growth, the wet and dry weights were assessed in control and in seedlings exposed to soil drought. Experiments to assess growth parameters were carried out in three biological replicates, each variant included at least 30 plants.

The contents of cytokinins (CK), indolylacetic acid (IAA) and abscisic acid (ABA) in 10 wheat seedlings (fresh weight 0.9-1.0 g) on days 7, 8 and 9 were determined by enzyme immunoassay (ELISA) test using specific rabbit antibodies and peroxidase-labeled anti-rabbit antibodies [15]. The seedlings were homogenized in 80% ethanol at a weight:volume ratio of 1:10, followed by incubation of the samples at 4 °C for 16 h. After centrifugation at 10,000 g for 20 mins (Avanti J-E centrifuge, Beckman Coulter, Inc., USA) the supernatant was evaporated in a stream of air to an aqueous residue, in an aliquot of which the total content of free cytokinins was determined. From the remaining aqueous residue, IAA and ABA were extracted with sulfuric ether, methylated with diazomethane, after evaporation, the dry residue was dissolved in 80% ethanol, and the IAA and ABA were quantigied in an aliquot. In details the procedure for purification and extraction of IAA and ABA, and the steps for phytohormone immunoassays have been described [15].

Extraction and quantification of free proline were carried out according to L.S. Bates et al. [16]. Samples of plant material (2 g) were poured with boiling distilled water (2.5 ml) and cooled. To 2 ml of a cold sample, 2 ml of ninhydrin reagent and 2 ml of glacial acetic acid were added. The mixture was boiled for 1 h and cooled. The color intensity of the proline complex with ninhydrin was measured at λ = 522 nm. The proline concetration was calculated using a calibration curve, which was constructed using chemically pure proline (Sigma Aldrich, USA).

The figures and tables present the arithmetic mean values (*M*) for three independent repetitions of an experiment, each carried out in three biological replicates, and their standard errors (±SEM). The results were processed statistically by ANOVA analysis of variance using SPSS 13.0 for Windows (SPSS, Inc., USA). The significance of the difference between the means was assessed by the LSD test at $p \leq 0.05$.

Results. Drought, as one of the most common unfavorable abiotic environmental factors, significantly reduces functional activity of cells in wheat plants, especially in the early development [17-19]. During this period, seeds and young seedlings are most susceptible to disturbances in the water regime.

In Russia, natural and artificial selection have produced two ecological groups of wheat, significantly different in drought adaptation strategies, the West Siberian forest-steppe ecotype and the Volga steppe ecotype. The regions of Western Siberia are characterized by spring drought, and therefore wheat plants of the forest-steppe West Siberian ecotype grow slowly at the initial stage of ontogenesis. In the southeastern regions of the European Russia, in particular, in the Volga region, drought occurs later, and varieties of the steppe Volga ecotype grow intensively at the beginning of the growing season to maximize root development.

1. Seed germination energy (%) **of wheat *Triticum aestivum* L. spring varieties Ekada 70 (steppe Volga ecotype) and Zauralskaya Zhemchuzhina (forest-steppe West Siberian ecotype) under different concentrations of sucrose solutions** (M±SEM, lab test)

Variety	Control	Sucrose solution, %		
		4	8	12
Ekada 70	91.1±3.9^{Aa}	80.2±3.4^{Ab}	71.1±3.1^{Ac}	40.7±1.7^{Ad}
Zauralskaya Zhemchuzhina	85.3±3.7^{Aa}	72.4±3.2^{Bb}	60.8±2.7^{Bc}	20.5±0.9^{Bd}

N o t e. Three experiments were carried out in triplicate with 15 seeds each. Different letters indicate statistically significant differences between options at $p \leq 0.05$ (ANOVA, LSD test). Large letters indicate differences in columns,

2. Length of the main root (cm) **in 3-day-old seedlings of wheat *Triticum aestivum* L. spring varieties Ekada 70 (steppe Volga ecotype) and Zauralskaya Zhemchuzhina (forest-steppe West Siberian ecotype) under different concentrations of sucrose solutions** (M±SEM, lab test)

Variety	Control	Sucrose solution, %		
		4	8	12
Ekada 70	2.95±0.13^{Aa}	1.91±0.08^{Ab}	0.86±0.04^{Ac}	0.23±0.01^{Ad}
Zauralskaya Zhemchuzhina	2.44±0.11^{Ba}	1.26±0.06^{Bb}	0.49±0.02^{Bc}	0.05±0.002^{Bd}

N o t e. Three experiments were carried out in triplicate (from 25 to 125 seedlings per variant). Different letters indicate statistically significant differences between options at p 0.05 (ANOVA, LSD test). Large letters indicate.

In the first series of our experiments, the drought resistance of plants was assessed by the seed germination energy (Table 1) and the length of the main root of 3-day-old seedlings (Table 2) in sucrose solutions of different concentrations (4, 8 and 12%), simulating drought. It was found that sucrose solutions simulating drought suppressed the germination of seeds of both wheat ecotypes, and germination energy decreased with increasing sucrose concentration.

The works of other researchers have shown that at early ontogenesis, the effect of dehydration leads to inhibition of seed germination and seedling growth, which subsequently significantly reduces wheat grain yield [20, 21]. It should be noted that the percentage of germinated seeds indicates the ability of plants to use hard-to-reach moisture and characterizes relative drought resistance of a certain variety. Thus, seeds of the Ekada 70 variety expressed a higher germination energy in concentrated sucrose solutions compared to the Zauralskaya Zhemchuzhina variety (see Table 1). These results confirm the previously reported data on the higher drought resistance of wheat of the steppe Volga ecotype at early ontogenesis [22].

Under dehydration conditions, the growth of the main root was inhibited in 3-day-old wheat seedlings of both ecotypes (see Table 2). However, on sucrose solutions, in the steppe Volga ecotype Ekada 70 variety the growth of the main root was inhibited significantly less than in seedlings of the Zauralskaya Zhemchuzhina variety.

Lab tests can only give an idea of the potential drought resistance of plants, while field trials or data obtained under conditions close to them are of practical importance. In this regard, we studied the effect of soil drought, which was modeled by the absence of irrigation, on growth in seedlings of different wheat ecotypes in a growing season. It was found that plants of the Ekada 70 variety in the control were characterized by an increased seedling mass throughout the entire period compared to the less drought-resistant variety of West Siberian selection (Fig. 1).

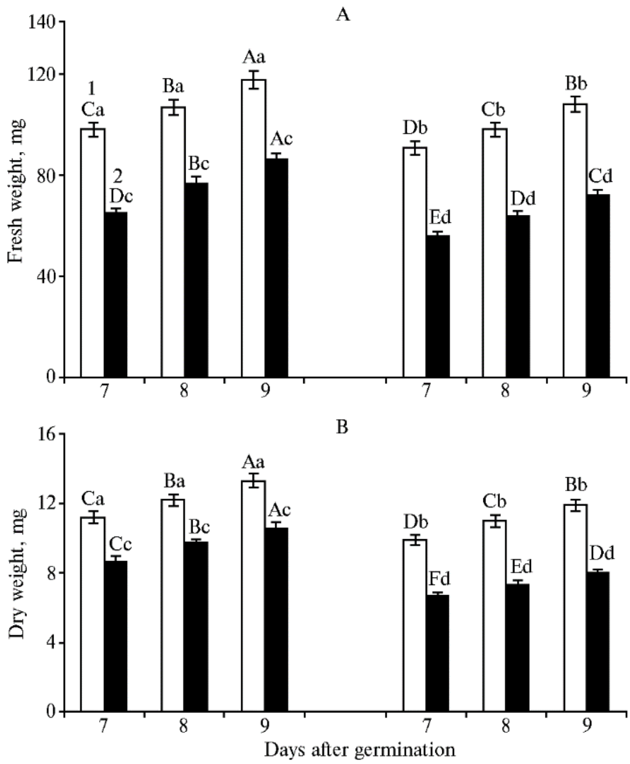

Fig. 1. Fresh (А) **and dry** (Б) **weight of 7-9-old seedlings in wheat** ***Triticum aestivum*** **L. spring varieties Ekada 70** (steppe Volga ecotype, left) **and Zauralskaya Zhemchuzhina** (forest-steppe West Siberian ecotype, right) **under simulated soil drought: 1** — control, **2** — treatment (M±SEM, pot trials). Three experiments were carried out in triplicate, each with 30 seedlings. Different lowercase letters indicate statistically significant differences between treatment variants for seedlings of the same age ($p \leq 0.05$, ANOVA, LSD test). Different capital letters indicate statistically significant differences between seedlings of different ages in the same treatment variant ($p \leq 0.05$, ANOVA, LSD test).

Soil drought led to a noticeable inhibition of growth rates in seedlings of both varieties, but in the Zauralskaya Zhemchuzhina variety it was more pronounced (see Fig. 1). It can be stated that wheat ecotypes with different strategies for adaptation to drought differ in their resistance to moisture deficiency at the initial stage of development. Plants of the steppe Volga ecotype are more drought-resistant compared to forest-steppe West Siberian ecotype. The changes that we observed in the studied ecotypes are due to genetic and ecological-physiological factors [9, 10].

The hormonal system plays a key role in the regulation of plant growth and development [23-25], and therefore it was of interest to trace changes in its state in the compared wheat varieties under soil drought conditions (Fig. 2). According to the results obtained, control plants of the resistant variety Ekada 70 accumulated a noticeably higher concentrations of auxin and cytokinins compared to the Zauralskaya Zhemchuzhina variety, while the concentration of ABA in both varieties was almost the same. Previously, many studies revealed a pronounced growth-stimulating effect of IAA and CK [15, 17]. That is is probably why in the Ekada 70 plants the growth rate parameters were highercompared to the Zauralskaya Zhemchuzhina (see Fig. 1). It is well known that under unfavorable conditions, in particular when the water regime is disturbed, significant changes occur in the plant hormonal balance with a sharp increase in the concentration of the stress hormone abscisic acid and a decrease in the level of growth-stimulating hormones auxins and cytokinins [17, 23, 26].

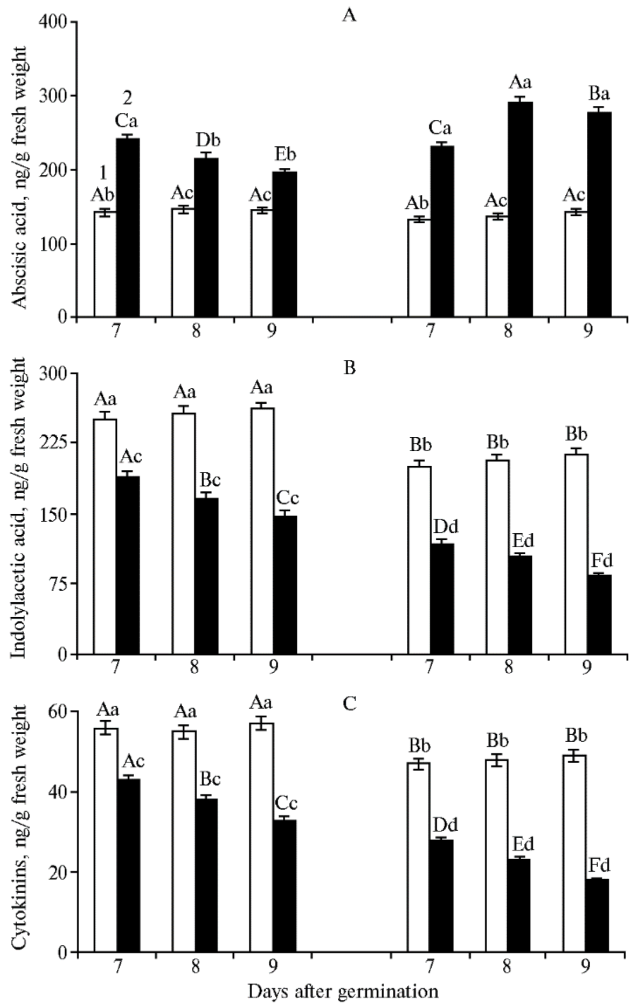

Fig. 2. Accumulation of abscisic acid (A)**, indolylacetic acid** (B) **and cytokinins** (C) **in 7-9-old seedlings of wheat *Triticum aestivum* L. spring varieties Ekada 70** (steppe Volga ecotype, left) **and Zauralskaya Zhemchuzhina** (forest-steppe West Siberian ecotype, right) **under simulated soil drought:** 1 — control, 2 — treatment (*M*±SEM, pot trials). Three experiments were carried out in triplicate, each with 10 seedlings. Different lowercase letters indicate statistically significant differences between treatment variants for seedlings of the same age ($p \leq 0.05$, ANOVA, LSD test). Different capital letters indicate statistically significant differences between seedlings of different ages in the same treatment variant ($p \leq 0.05$, ANOVA, LSD test).

Indeed, it can be seen (see Fig. 2) that growing wheat under simulated soil drought conditions also led to changes in the hormonal status of seedlings in both studied varieties. There was an accumulation of ABA and a noticeable decrease in the concentrations of IAA and CK, but the studied varieties differed in these indicators. Thus, in the drought-resistant variety Ekada 70, the maximum 2-fold accumulation of ABA in seedlings occurred only on day 7, followed by its gradual decrease. In the variety Zauralskaya Zhemchuzhina, more than 2-fold stress-induced accumulation of ABA in seedlings remained until the end of the test. The impact of soil drought led to a progressive decrease in the concentration of IAA and cytokinins in seedlings of both varieties, but in Zauralskaya Zhemchuzhina variety, by the end of the experiment (9 days), the content of IAA and cytokinins was almost 2.5 times lower than the control values (see Fig. 2). That is, when the water regime was disrupted, a sharp imbalance of phytohormones occurred in plants of the Zauralskaya

Zhemchuzhina variety which led to a pronounced growth inhibition. Plants of the Ekada 70 variety showed resistance to moisture deficiency due to significantly lower stress-induced changes in the hormonal system.

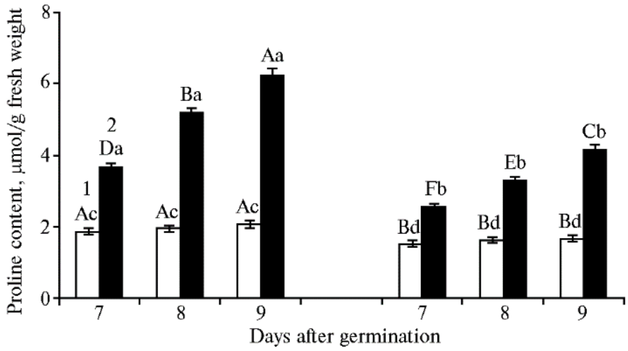

Fig. 3. Proline content in 7-9-old seedlings of wheat *Triticum aestivum* L. spring varieties Ekada 70 (steppe Volga ecotype, left) **and Zauralskaya Zhemchuzhina** (forest-steppe West Siberian ecotype, right) **under simulated soil drought:** 1 — control, 2 — treatment (M±SEM, pot trials). Three experiments were carried out in triplicate, each with 20 seedlings. Different lowercase letters indicate statistically significant differences between treatment variants for seedlings of the same age ($p \leq 0.05$, ANOVA, LSD test). Different capital letters indicate statistically significant differences between seedlings of different ages in the same treatment variant ($p \leq 0.05$, ANOVA, LSD test).

Since the moisture deficiency causes both a violation of the water regime and osmotic stress, we compared the levels of proline as the effective osmoprotector in wheat seedlings of two varieties (Fig. 3). In controls, the proline content remained relatively stable throughout the experiment, although in the roots of the Zauralskaya Zhemchuzhina plants were distinguished by a slightly lower proline content (see Fig. 3). In both varieties, in seedlings under soil drought, a significant progressive accumulation of proline occurred compared to control (see Fig. 3), which indicates the participation of this amino acid in protecting plants from dehydration. Thus, in the Ekada 70 variety, in stressed seedlings by day 9 of the experiment, the proline content increased more than three times compared to control. In the Zauralskaya Zhemchuzhina variety, stress-induced proline accumulation in seedlings was also found but its absolute values were inferior to those in the Ekada 70 (see Fig. 3).

As is known, drought causes a decrease in the osmotic potential of plants, which induces the accumulation of proline as one of the key osmolytes [27, 28]. Many studies have shown that an increase in proline content provided an increase in plant stress resistance [29, 30]. Moreover, the proline accumulation helps reduce the concentration of reactive oxygen species and significantly reduces membrane damage from adverse factors, including drought [31]. There is a positive correlation between increased proline levels and plant resistance to extreme conditions. We found that normally the seedlings of the drought-resistant Ekada 70 variety contained 25-30% more of this osmoprotector than the Zauralskaya Zhemchuzhina variety (see Fig. 3). Under simulated soil drought, in both varieties there was a progressive accumulation of proline in the seedlings, being although more than 1.5 times higher in the drought-resistant Ekada 70 compared to Zauralskaya Zhemchuzhina, which probably contributes to a more pronounced resistance of steppe Volga ecotype to drought during early ontogenesis.

Thus, our findings indicate that at the initial stage of plant development the varieties Zauralskaya Zhemchuzhina (forest-steppe West Siberian ecotype) and Ekada 70 (steppe Volga ecotype) differ in their resistance to moisture deficiency. Under drought conditions, the Ekada 70 had higher seed germination energy and seedling growth rates, that is, this variety showed greater drought resistance compared to the Zauralskaya Zhemchuzhina variety. Differences in drought resistance of the ecotypes may be due to different responses of the hormonal system to moisture deficiency. Plants of the Zauralskaya Zhemchuzhina variety show much more pronounced stress-induced changes in hormonal balance, which led to a greater growth inhibition. The ability of the Ekada 70 variety to induce a significant accumulation of the amino acid proline, an important plant defender, significantly contributs to a higher drought resistance.

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