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IMPACT OF HIGH TEMPERATURE ON GROWTH OF EMBRYO AND GERMINATION OF HETEROMORPHIC SEEDS OF *Anethum graveolens* L. (*Apiaceae*)

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Abstract

Heteromorphism is widespread in nature and manifests itself in the variation of various parameters of seeds within individual individuals and populations. Dill (*Anethum graveolens* L.) seeds are characterized by heteromorphism caused by the maternal factor. First of all, the maternal factor effects on the size of the seeds, in this case a variation in the size of the embryo can be observed. The study of the reaction of such seeds to the action of abnormal weather conditions is an urgent task. High temperature is one of the unfavorable abiotic factors that plants can be exposed to at different stages of development. In the present study, a significant thermal sensitivity to the long-term effect of suboptimal (higher than the optimal) temperature of embryos from dill seeds, formed in inflorescences of the second order of branching, was revealed for the first time. Under the influence of high temperature, the growth of embryos was inhibited. As a result, germination of intact dill seeds obtained from second-order inflorescences was observed. This work is devoted to the study of the effect of high temperature on the growth of the embryo and the germination of intact dill seeds obtained from different orders of branching. The study aimed to determine the influence of the maternal factor, as well as high temperature on the growth of the embryo during germination and on the germination of intact dill seeds formed in inflorescences of different orders of branching. The research was conducted in 2015-2016 at the All-Russian Research Institute for Vegetable Growing, Branch of the Federal Scientific Vegetable Center, with the late-ripening dill variety Centaur seeds, formed in inflorescences of the first and second orders of branching. The seeds were obtained from dill plants grown in the open field. Harvesting was carried out on day 50 after flowering of 1st order umbels. The experiments were carried out in a temperature-controlled thermostat. To determine the critical temperature for the growth of the embryo during germination and germination rate of intact seeds formed in different orders of branching, a wide temperature range was applied, 20 °C as control, and 25, 30, 35 and 40 °C. Using the morphometric method of analysis, we studied the growth of the embryo, as well as the dynamics of the germination of intact seeds against the high temperatures background. The data obtained were used to calculate the parameters and plot the embryo growth curve, as well as the germination curve of intact seeds. Logistic regression was used to calculate the maximum suboptimal temperature at which embryo growth and seed germination are possible. On the basis of experimental data, we have shown that embryos, formed at different branching orders of the mother plant, have different stages of development. The initial dimensions of the embryo of the first branching order are 30 % higher than the second ($p < 0.001$). Under the action of a temperature of 30-35 °C, differences appeared in the thermal sensitivity of the embryos and the growth rate of the embryos. The effect of high temperatures is crucial for the growth of the embryo (57.0 %; $F = 415.3$, $p < 0.001$) and germination of dill seeds (37.2 %; $F = 270.5$, $p < 0.001$). The maximum temperature at which the growth is possible is 40 ± 0.4 °C for the first-order embryo, and 38 ± 0.5 °C for the second-order embryo ($p < 0.001$). The maximum temperature allowing for germination of at least 50 % of

viable first-order seeds is 34 ± 0.3 °C, for the second-order 30 ± 0.4 °C ($p < 0.001$). The seeds are more sensitive to high temperatures than the embryos, and the growth of the embryo has a significant effect on seed germination ($r = 0.946$; $t = 25.85$; $p < 0.001$). Our studies have shown that the temperature sensitivity of second-order embryos, which is clearly manifested against the background of morphological underdevelopment, is one of the main reasons for the slow, inhomogeneous and incomplete germination of the dill seed population under suboptimal temperature conditions.

Keywords: *Anethum graveolens* L., embryo growth, heteromorphism, seed position, mother plant, seed germination, thermosensitivity

Heteromorphism which refers to the appearance on one plant of seeds that differ in size, weight, color, morphology, anatomy, germination and other characteristics is widely represented in the plant world and inherent in both wild and cultivated forms [1-3]. In the families *Asteraceae*, *Chenopodiaceae*, *Poaceae*, *Apeaceae*, and *Brassicaceae*, the seed size varies significantly [4-7]. Some species, for example *Danthonia spicata* [8] and *Heterosperma pinnatum* [9], show a discrete variability, while others, in particular *Rubus ulmifolius* [10], *Raphanus raphanistrum* [11], and *Rubus chamaemorus* [12], show permanent variation in seed size.

Between individuals [13-15] and in the population [16, 17], the variability of seeds in terms of a set of characters, including sowing qualities [18-20], is widespread. Different germination capacity and requirements, as a rule, are associated with the location of seeds formed on different metameres of the mother plant. One of the main explanations for these differences is that the nutritional resources of the mother plant are not equally distributed among the seeds [21]. In addition, seed formation differs temporally and, therefore, occurs under different weather conditions. Moreover, the age, physiological and biochemical state of the mother plant also change, which additionally affects the seed metabolism [22].

Heteromorphism caused by the maternal factor is widespread among vegetable crops of the family *Apiaceae* [23, 24]. These plants are characterized by extended flowering and seed maturation in umbels. Hendrix [25] showed that the size and weight of parsnip seeds decrease as the branching order increases. Thompson notes [26] that the variation in seed size within a single *Lomatium grayi* plant reaches 16%. The influence of heteromorphism of *Apiaceae* seeds on their quality has been studied by many researchers. Thomas et al. [27] found that carrot seeds collected from primary and secondary umbels are unequal in quality parameters under different conditions of germination. In the same work, the influence of the branching order on the manifestation of dormancy in *Apium graveolens* seeds and their sensitivity to GA_{4/7} was revealed. Many papers have shown that the quality of carrot seeds decreases as the branching order increases [28-30].

Morphologically underdeveloped embryo is among the key endogenous factors which affect quality of the *Apiaceae* seeds [31-33] and impose special requirements for their use. Various conditions can inhibit embryonic growth at several critical stages and thus affect the seed germination rate and the number of germinated seeds. Plant adaptive responses are attracting urgent scientific interest due to current climatic instability and the likelihood of abnormal weather conditions. For example, plants can be exposed to high temperatures at different stages of development [34]. The influence of this factor on seed germination is considered from the point of view of cardinal temperatures [35, 36].

For seeds of most crops, the temperature optimum ranges from 15 to 30 °C with the maximum from 30 to 40 °C [35]. For embryos and intact dill seeds formed in inflorescences of the first and second branching orders, the cardinal temperature has not been determined. In most works, the influence of seed location in the umbel on seed quality and germination parameters [28-30] and the effect of high temperature on seeds [37, 38] were studied on carrot plants. Fewer

similar studies have been conducted on dill [39]. The growth of the embryo in the seeds after separation from the mother plant was assessed mainly on wild *Apiaceae* species [40, 41]. The pre-development of embryos from different branching orders in umbels and the influence of stress factors on this process in the *Apiaceae* seeds, in particular in dill, is poorly covered.

Previously, we considered the germination features and kinetic parameters at different temperatures in homogeneous lots of seeds of vegetable umbellifers [42].

In this work, for the first time, we revealed a significant thermal sensitivity of embryos from seeds of second-order umbels to the long-term exposure to superoptimal temperature. High temperatures inhibit the embryo growth and, consequently, the germination of intact dill seeds derived from the second-order inflorescences.

The work aimed at studying effects of seed position in an umbel and high temperatures on embryo growth and germination of intact dill seeds.

Materials and methods. Dill (*Anethum graveolens* L.) late-season cv. Centaur plants were grown in the field (Moscow region, 55°36'N 38°1'E, the All-Russian Research Institute of Vegetable Growing — a Branch of Federal Research Center for Vegetable Growing, 2015-2016). The cv. Centaur plants in the flowering phase are 100-110 cm in height, spreading and leafy, the umbels are large in size, convex, and multi-radial. In the conditions of the Moscow region, cv. Centaur plants form mature umbels on the axes of two orders. To produce seeds derived from first-order (1o) and second-order (2o) umbels, the sowing was performed in the second decade of May (10 m² plots allocated randomly, 45×10 cm rows, a 1.5 cm seeding depth, and the 1-2 g/m² seeding rate). Experiments were arranged in triplicate.

Harvesting was carried out on day 50 after the 1o umbel flowering began. Two-order umbels were cut off 90 selected plants. The seeds were dried and stored under natural conditions in the laboratory for 6 months. After storage, the moisture content and 1000-seed weight were measured.

The temperatures critical for embryo growth in intact 1o and 2o germinating seeds were determined within the following rang: 20 °C (control) refers to as the average optimum temperature for non-dormant seeds [43], 25, 30, 35, and 40 °C (a TC 1/80 thermostat, OJSC Smolenskoye SKTB SPU, Russia). The substrate was constantly kept moist, the air humidity in the chamber was 90-95%. Before the test, seeds were sterilized with 0.125% sodium hypochlorite for 5 min and rinsed in distilled water. The tests continued for 21 days in the dark.

To assess the embryo growth dynamics, the intact seeds were placed into 9-cm Petri dishes on a sheet of filter paper moistened with distilled water (four replicates of 10 seeds per day). Additional portion of seeds (four replicates, 100 seeds each) were provided to be randomly selected, if necessary, in case of seed death or appearance of embryo-less seeds. For each treatment, the seeds in Petri dishes selected daily at random were cut with a blade and the embryos were removed. Approximately 6,000 seeds were examined. The seeds were cut in half, the embryo length was measured. In germinated seeds, the critical embryo length parameter was used, i.e., the length of the embryo after the rupture of the seed coat but before the root appears [44]. Embryos were imaged using a Levenhuk 670T microscope (Levenhuk, USA) with a 4× achromatic objective connected to a ScopeTek DCM 300 MD video eyepiece (ScopeTek, China). The embryo length was measured using the Scope Photo image analysis software (Image Software V. 3.1.386), the endosperm length was measured with a caliper, and the embryo length (E) to endosperm length (S) (E:S) ratio was calculated. The E:S ratio was scored as follows: 1 — 0.0-0.19 (the embryo is less than 1/4 of the endosperm in length, the heart stage); 2 — 0.20-0.29 (the embryo is 1/4 of the endosperm in

length, the cotyledon and the root are of equal length); 3 — 0.30-0.39 (the embryo is approximately $\frac{1}{3}$ of the endosperm in length, it has pronounced cotyledons and the root); 4 — 0.40-0.59 (the embryo is $\frac{1}{2}$ of the endosperm in length, the root is longer than the cotyledons); 5 — 0.60-0.79 (the embryo is $\frac{2}{3}$ of the endosperm in length); 6 — 0.80-1.00 (the embryo and the endosperm are almost equal in length) [45].

The effect of high temperature on seed germination was assessed in a 21-day test by the radicle protrusion. Radicle emergence was considered as the completion of germination. In the test, portions of intact seeds (4 replicates, 100 seeds each) were germinated as described above. The number of seeds with a visible protrusion of radicle was counted daily. In total, approximately 4000 seeds were examined. Sprouted seeds were removed.

The data were used to construct graphs of embryo growth and seed germination. For embryo growth, the four-parameter logistic regression was applied where b was the slope of the embryo growth graph, c was the lower point of the embryo growth graph which corresponds to the initial embryo length, d was the upper point of the embryo growth graph which corresponds to the maximum embryo length during germination, e was the period (in days) during which the embryo reached 50% length necessary for seed germination. To plot the seed germination graph, the three-parameter logistic regression was used where b was the slope of the seed germination graph, d was the upper point of the seed germination graph which corresponds to the percentage of germinated seeds during the test; e was the period (in days) during which germination of 50% of all germinated seeds occurred [46, 47]. Logistic regression was used to calculate the maximum temperature at which embryo growth and seed germination are possible.

Differences were statistically assessed using the standard error (\pm SEM) and criteria for the null hypothesis that the difference was 0. All data were tested for normality of distribution (W, Shapiro-Wilk test). Two-way analysis of variance with preliminary conversion to the root of the arcsine angle was used to assess the influence of the studied factors on the embryo growth and seed germination. The relationship between parameters was assessed using Pearson's correlation analysis. Differences in each pair of compared values were considered statistically significant at $p \leq 0.05$. The presented models were implemented in the drc extension package for the R software environment. All statistical analyzes were performed in R version 3.4.3 [48].

Results. For 1o and 2o umbels, the 1000-seed weigh was 1.50 and 1.32 g, respectively, in 2015 and 1.59 and 1.41 g, respectively, in 2016. The moisture content in seeds after drying was 12-13%.

An increase in the temperature to the maximum (40 °C) inhibited the embryo growth in both 1o and 2o seeds ($p < 0.001$) (Fig. 1). A less aggressive temperature (30-35 °C) disclosed differences in the thermal sensitivity of embryos. Comparison of their growth graphs clearly reveals heteromorphism of the initial length ($p < 0.001$). The inhibition of the growth was expressed during germination in a decrease in their maximum length from 2.30 ± 0.02 mm (E:S = 0.68) at 20 °C to 1.21 ± 0.04 mm (E:S = 0.36) at 40 °C for 1o seeds and from 1.89 ± 0.03 mm (E:S = 0.62) at 20 °C to 0.86 ± 0.01 mm (E:S = 0.28) at 40 °C for 2o seeds. High temperatures negatively affected the growth rate of embryos. As the temperature rose from 20 to 25 and 35 °C, the time embryos needed increased by 2.4 ± 0.3 ($p < 0.001$) and 5.3 ± 0.9 days ($p < 0.001$), respectively, for 1o seeds and by 2.9 ± 0.8 ($p < 0.001$) and 3.1 ± 1.2 days ($p = 0.007$), respectively, for 2o seed. The growth rates of 1o and 2o embryos under the same stress differed insignificantly. With an increase in temperature to 40 °C, the growth of embryos in seeds of both orders

completely stopped in 4-5 days.

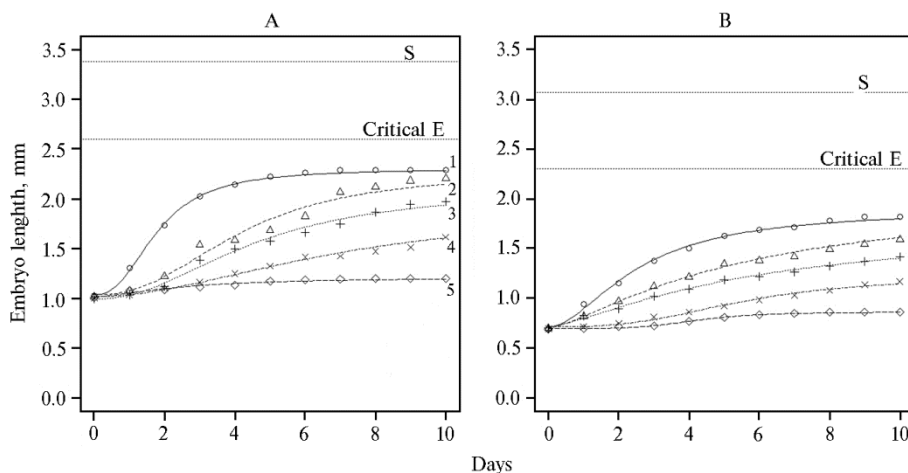


Fig. 1. Embryo growth during dill (*Anethum graveolens* L.) late-season cv. Centaur seed germination as influenced by high temperature and the umbel order on the mother plant: A — first-order umbels, B — second-order umbels; 1 — 20 °C, 2 — 25 °C, 3 — 30 °C, 4 — 35 °C, 5 — 40 °C; S — endosperm length, Critical E — critical embryo length (lab tests, 2015-2016).

An increase in temperature also resulted in inhibition of seed germination ($p < 0.001$), which was expressed in a decrease in the germination rate and the number of germinated seeds (Fig. 2). The average percentage of germination for 1o seeds decreased with an increase in temperature to 30 and 35 °C compared to 20 °C (by $16.0 \pm 0.7\%$, $p < 0.001$ and $46.0 \pm 0.8\%$, $p < 0.001$, respectively). The percentage of germination of 2o seeds also decreased significantly ($p < 0.001$). At 20 °C, the percentage of germination of 1o seeds was $19.0 \pm 0.63\%$ ($p < 0.001$) higher than that of 2o seeds. At 30 and 35 °C, germination of 2o seeds compared to 1o seeds decreased 2.1-fold and 5.2-fold, respectively ($p < 0.001$). The 50% germination period for 1o seeds at 30 and 35 °C was 2.3 ± 0.1 ($p < 0.001$) and 3.5 ± 0.2 days ($p < 0.001$) longer than at 20 °C. For 2o seeds at 30 °C, this time increased by 3.7 ± 0.2 days ($p < 0.001$) compared to 20 °C.

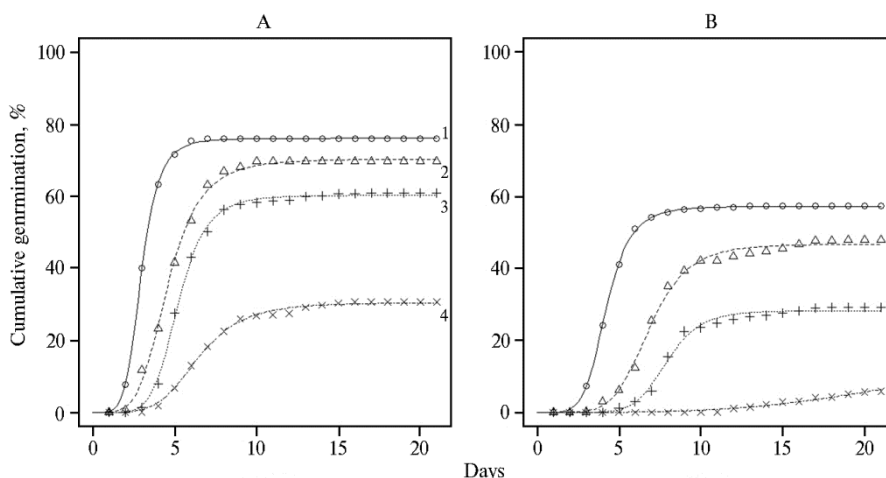


Fig. 2. Germination of dill (*Anethum graveolens* L.) late-season cv. Centaur seeds as influenced by high temperature and the umbel order on the mother plant: A — first-order umbels, B — second-order umbels; 1 — 20 °C, 2 — 25 °C, 3 — 30 °C, 4 — 35 °C (at 40 °C, no germination occurred; lab tests, 2015-2016).

The maximum embryo length in germinating seeds had a significant effect

on the number of germinated seeds (the Pearson correlation coefficient $r = 0.946$, $t = 25.85$; $p < 0.001$). Two-way analysis of variance revealed a significant influence of several factors, i.e., the high temperature (57%, $F = 415.3$, $p < 0.001$), the location on the mother plant (37.2%, $F = 270.5$, $p < 0.001$), the year of growing (5.3%, $F = 38.5$; $p < 0.001$), and their interaction (0.37%, $F = 2.7$, $p = 0.004$) on the maximum embryo length during seed germination. The data show that the year had the smallest influence. The high-temperature factor (71.0%, $F = 1013.1$, $p < 0.001$), the location on the mother plant (27.6%, $F = 395.1$, $p < 0.001$), the year of growing (0.9%, $F = 12.9$, $p = 0.001$), and the interaction of these factors (0.7%, $F = 10.1$, $p < 0.001$) had a significant effect on the percentage of germinated seeds. As seen, the effect of high temperature was of decisive importance for the embryo growth and germination of intact dill seeds.

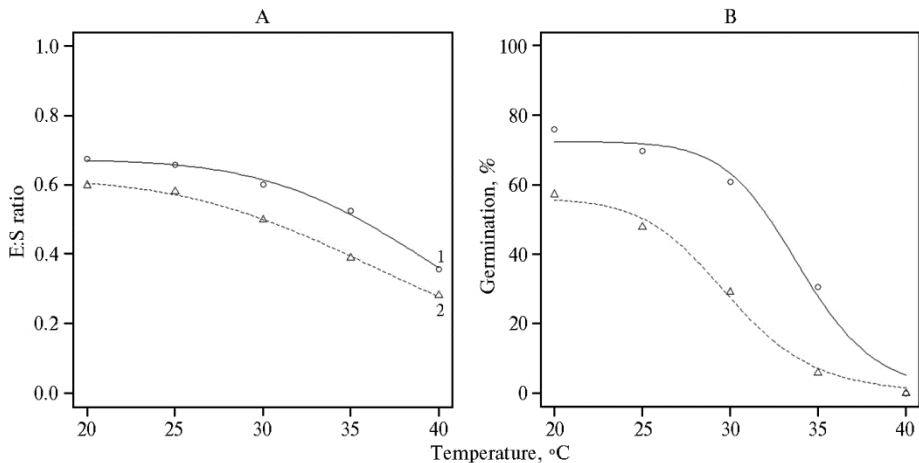


Fig. 3. Dose—response relationship between temperature and maximum embryo length in dill (*Anethum graveolens* L.) late-season cv. Centaur seeds during germination (for more correct interpretation, embryo length to the endosperm length E:S ratio was used for recalculation) (A) and percentage of germinated seeds (B) depending on the umbel order: A — first-order umbels, B — second-order umbels lab tests, 2015-2016).

The maximum temperature which allows embryos growth is 40 ± 0.4 °C, for 1o seed and 38 ± 0.5 °C for 2o seeds ($p < 0.001$). The maximum temperature, allowing for radicle emergence in at least 50% of viable seeds, was 34 ± 0.3 °C for 1o and 30 ± 0.4 °C for 2o ($p < 0.001$) (Fig. 3).

Differentiated embryos in mature seeds is characteristic of the *Apiaceae* crops, however, a certain proportion of seeds have embryos underdeveloped to varying degrees. Their further development occurs after the seed separation from the mother plant, i.e., during germination, and has its own characteristics [49, 50]. We have shown that embryos from seeds of different orders differ not only in length, but also in E:S ratios. The initial E:S value for the 1o embryos was 0.31 ± 0.01 . They had pronounced cotyledons and root. For the 2o embryos, the initial ratio was 0.23 ± 0.01 , and the cotyledons and root were of equal length and weakly developed. That is, already at the early germination, the 1o embryos had an advantage over the 2p embryos. Larger 1o seeds accumulated more nutrients and had a potential resource for maintaining higher growth rate of the embryo. According to the data obtained, in order the radicle to be emerged, the embryo should lengthen at least by 40-50% of its original length. In this case, the growth rates of the embryo (see Fig. 1) under conditions of optimal and stress temperatures significantly differed depending on seed location. As a result, the number of germinated 1o seeds was higher than that of 2o seeds (see Fig. 2).

Under unpredictable growing conditions, temporal separation of seed

ripening or germination effectively reduces the risk of offspring death and increases reproductive success. It can be expected that the role of varying the morphometric parameters of seeds within individual plants will increase if the environment is unpredictable [51-53]. Consequently, from an evolutionary point of view, seed heteromorphism is an adaptively positive phenomenon. However, in agronomic practice, as a rule, it becomes the cause of a decrease in the number and rates of seed germination, thinness of stands, heterogeneity of seedlings and plants [54, 55]. The problem of heteromorphism can be addressed by improving the production and processing of seeds.

Heat stress is one of the most significant abiotic factors that determine the productivity of many agricultural crops [56-58], in particular celery [59, 60]. It is believed that exceeding the optimal temperature for a particular plant species by 10-15 °C causes a cascade of responses aimed at transmitting a stress signal and increasing resistance, which is expressed in a shift in metabolic reactions and physiological processes [61-63]. Non-dormant seeds can usually germinate over a wide range of temperatures. However, a constant temperature of about 40 °C during the swelling period turns out to be critical for seeds of many species and makes germination difficult [64].

We revealed a significant sensitivity of dill embryos to high temperatures, depending on the order of umbels. The physiological response to the continuous action of elevated temperatures (30-40 °C) was a progressive inhibition of embryonic growth and seed germination. At temperatures from 25 to 35 °C, differences were observed in the response of embryos and seeds to stressors. The growth of the embryo and germination slowed down to one degree or another with an increase in the swelling temperature to 30-35 °C for 1o seeds and up to 25-30 °C for 2o seeds.

The effect of temperature on seed germination has been studied in several works [65-67]. In particular, the combination of factors of salinity, water and temperature regimes for seed germination was studied [68-70]. However, the influence of the embryo diversity due to location on the mother plant on the resistance to high temperatures during germination was not considered. In our experiments, the maximum germination temperature, allowing for radicle emergence in at least 50% of viable seeds and embryo growth, differed significantly depending on seed orders. As the critical temperature (40 °C) was approached, the differences leveled off. Embryos in 1o and 2o seeds exhibited significant sensitivity to prolonged and continuous exposure to elevated temperatures during swelling and were not capable of germination at 40 °C. Intact seeds were found to be more sensitive to high temperatures than embryos.

Germination rate is another important aspect of the seed germination process which can be temperature dependent. Our results showed that, for dill, the germination rate of intact seeds increased linearly in the temperature range to their optimum value, and then decreased. Similar linear relationships between the germination rate and temperature were observed in millet [71], *Kochia scoparia* [72], cuphea [73], *Plantago ovata* [74], and some medicinal plants [75]. We found significant differences in the germination rate of 1o and 2o dill seeds under high temperature stress.

The thermosensitivity of embryos, due to their morphological underdevelopment, is one of the main reasons for the slow, inhomogeneous and incomplete germination of the seed population under superoptimal temperature conditions. Modeling the process of germination of seeds with an underdeveloped embryo is of interest both for breeding practice and for improving seed pre-sowing processing. Methods based on the kinetics of embryo growth and germination of

heteromorphic dill seeds under a wide range of temperature can be useful in breeding for heat resistance

Thus, the initial development of dill embryos of the cv. Centaur during formation of seeds on the mother plant affects their germination. Embryos from seeds derived from umbels of different orders (first-order — 1o, second-order — 2o) differ in morphometric parameters. The 1o embryos were significantly larger than 2o embryos in initial size. The 1o embryos are better developed and less sensitive to high temperatures during germination. High temperatures significantly influence the embryo growth rate, seed germination, and the number of germinated seeds. The seeds are more sensitive to high temperatures than the embryos. Significant differences in the thermal sensitivity of embryos and intact seeds due to location on the mother plant that we revealed during germination occur already at 20-30 °C. The temperature which rises to 35-40 °C inhibits embryo growth and seed germination regardless of the umbel orders. In dill cv. Centaur, the maximum temperature for the 1o embryos was significantly higher than for the 2o embryos. Our study has shown that the temperature factor largely determines embryo development prior to seed germination and can be an effective for pre-sowing seed treatment.

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