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Effect of low positive temperature on the antioxidant system formation in de-etiolated and etiolated *Amaranthus tricolor* L. seedlings grown from seeds treated with growth regulators

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Abstract. In the Non-chernozem zone of Russia, the recurrent spring cold up to 1–2 °C can cause damage and death of thermophilic amaranth seedlings. Pre-sowing treatment of seeds with growth regulators is an inexpensive and effective method to reduce the negative effect of hypothermia on seed germination. The aim of the research was to study the effect of low-temperature stress on etiolated and de-etiolated seedlings of amaranth cv. 'Valentina' (*A. tricolor* L.) grown from seeds treated with growth stimulants. Seeds were pretreated with aqueous solutions of Albit (1 g/L), hydrogen peroxide (H_2O_2) — 5 mM and succinic acid (ScA) — 500 mg/L. Seeds were germinated in peat pots at 23 ± 2 °C (T_{23}) for 7 days. On the 7th day, peat pots with seedlings grown in the light and in the dark were moved to thermostat at 2.0 ± 0.5 °C (T_2) for 8 hours. Determination of the amount of amaranthine, chlorophylls and carotenoids were carried out according to generally accepted methods. Pretreatment of seeds with the growth regulators Albit, H_2O_2, and ScA increased hypocotyl length, root length, and biomass of light and etiolated seedlings. Low positive temperatures increased the content of amaranthine and carotenoids but reduced the content of chlorophylls. It was shown that all used growth regulators — H_2O_2, Albit and ScA — trigger or at least maintain the system of antioxidant protection in light and etiolated seedlings of amaranth cv. 'Valentina' under low positive temperatures.

Keywords: Valentina, cultivar, amaranthine, photosynthetic pigments, abiotic stress, low-temperature stress, chlorophyll

Conflicts of interest. The authors declared no conflicts of interest.

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Introduction

Low temperatures are among the main abiotic stresses that significantly reduce yield and affect almost all plant functions such as photosynthesis, water and nutrient uptake, transpiration and respiration [1, 2].

Amaranth (*Amaranthus tricolor* L.) is a leafy vegetable plant containing biologically active compounds with antioxidant activity, including ascorbic acid, amaranthine, β-carotene, phenols and flavonoids [3]. In the Non-chernozem zone of Russia, the recurrent spring cold up to 1–2 °C can cause damage and death of thermophilic amaranth seedlings. It is known that low-temperature stress induces accumulation of reactive oxygen species (ROS) such as superoxide radical, hydrogen peroxide, singlet oxygen and hydroxyl radicals [4, 5]. Damage caused by ROS and disruption of cellular homeostasis are facilitated by the action of various antioxidants: enzymatic (catalase, superoxide dismutase, peroxidase, glutathione reductase, glutathione peroxidase) and non-enzymatic (ascorbic acid, carotenoids, alpha-tocopherols and glutathione) [4, 5]. The mechanism of ROS formation and their neutralization by low molecular weight antioxidant system were associated with resistance of plants to abiotic stresses [6].

Currently, much attention is paid to the development of approaches to reduce the negative effects of abiotic stresses on seed germination. Pre-sowing treatment of seeds with growth regulators is inexpensive and effective method [7]. Seed pre-treatment is an induction of a certain physiological state, in which plants are able to activate protective reactions faster and better to cope with abiotic stress [7, 8].

Plant responses to abiotic stresses, including low positive temperatures, have been the subject of various studies for several decades. The study of plant responses to stressors is necessary to understand adaptation of plants grown in the open ground [9]. At the moment, there are not enough data in literature on how the antioxidant system in amaranth seedlings responds to low positive temperatures, and what is the importance of pre-sowing treatment for practical use.

The aim of the study was to investigate the effect of low-temperature stress on light and etiolated seedlings of amaranth cultivar 'Valentina' (*A. tricolor* L.) grown from seeds treated with growth regulators.

Materials and methods

Seeds and seedlings of vegetable amaranth *Amaranthus tricolor* L., cv. 'Valentina', selected in Federal Scientific Center for Vegetable Growing (Moscow Region) were studied.

Seed pretreatment. Homogeneous and complete seeds were carefully selected. 4 variants of seed treatments were studied: Albit (1 g/L), hydrogen peroxide (50 mM/L), succinic acid (500 mg/L). Distilled water was used as control. Seeds were soaked in solutions for 4 hours, then washed with distilled water, dried, and sown into peat pots. A part of the pots was covered with a material that does not transmit light and placed in a dark room. The experiment was performed in three replications. Plants were grown at 23 ± 2 °C (T_{23}). On day 7, peat pots with seedlings grown in the light and in the dark were moved to a thermostat at 2.0 ± 0.5 °C (T_2) for 8 hours (overnight).

Biochemical parameters. The content of photosynthetic pigments was determined by spectrophotometric method. The total content of chlorophylls and carotenoids was calculated by the formulas [10].

$$\text{Хл а}\left[\frac{\text{мг}}{\text{г}}\right] = \frac{\left(13{,}36A_{664{,}2} - 5{,}19A_{648{,}6}\right)V}{1000m};$$

$$\text{Хл б}\left[\frac{\text{мг}}{\text{г}}\right] = \frac{\left(27{,}43A_{648{,}6} - 8{,}12A_{664{,}2}\right)V}{1000m};$$

$$\text{Кар}^{\Sigma}\left[\frac{\text{мг}}{\text{г}}\right] = \frac{\left(4{,}785A_{470} + 3{,}657A_{664{,}2} - 12{,}76A_{648{,}6}\right)V}{1000m},$$

where A_{470}, $A_{648,6}$ and $A_{664,2}$ — absorbance at 470 nm, 648.6 nm and 664.2 nm respectively; V = volume of extract (ethanol 96 %) in ml; m = weight of the sample in g.

The amount of amaranthine in the water extracts was determined considering a molar extinction coefficient of 5.66·104 $l{\cdot}mol^{-1}{\cdot}cm^{-1}$ and a molar weight of 726.6 $g{\cdot}mol^{-1}$ [11].

Data analysis. Data were presented as the mean of three replications ± SD (standard deviation) at a significance level of $P \leq 0.05$. Data analysis was performed in the R environment [12].

Photographs of cotyledon leaves and hypocotyls were taken using a Stemi 508 inverted stereomicroscope with an Axiocam 305 color camera (Carl Zeiss Microscopy GmbH, Germany) at 5× magnification.

Results and discussion

Effect of pre-sowing treatment on morphometric parameters of seedlings. The present study revealed that pre-sowing treatment of amaranth seeds with plant growth regulators improved morphometric parameters of amaranth seedlings grown under light and dark conditions (Table 1).

Table 1

Morphometric parameters of amaranth cultivar 'Valentina' seedlings grown from seeds treated with growth regulators under light and dark conditions

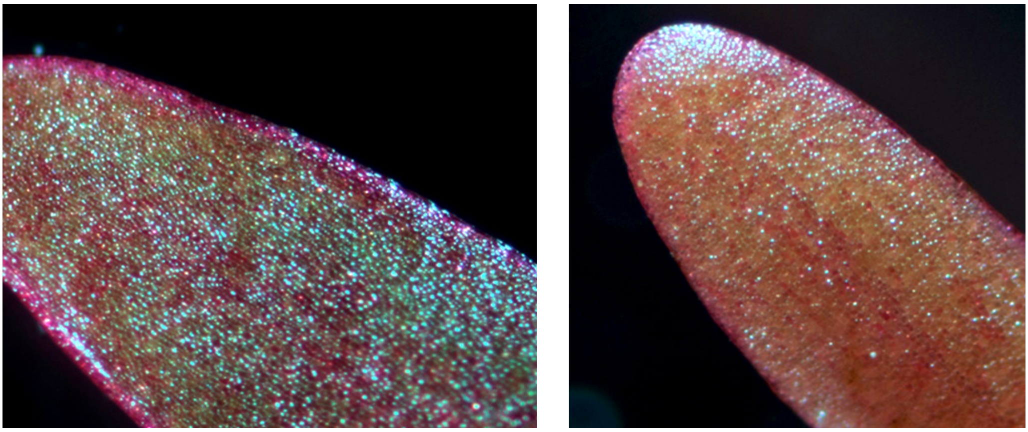
Variant	Light conditions			Dark conditions		
	Hypocotyl length, cm	Root length, cm	10-seedling weight, g	Hypocotyl length, cm	Root length, cm	10-seedling weight, g
H_2O (Control)	2.53 ± 0.18	2.28 ± 0.32	0.0780 ± 0.0022	6.12 ± 0.21	2.10 ± 0.43	0.1003 ± 0.0070
Albit	3.28 ± 0.21	3.53 ± 0.35	0.0890 ± 0.0027	7.10 ± 0.14	2.62 ± 0.38	0.1120 ± 0.0075
Succinic acid	2.78 ± 0.084	4.01 ± 0.27	0.0787 ± 0.0020	6.20 ± 0.15	3.28 ± 0.40	0.1033 ± 0.0043
H_2O_2	2.87 ± 0.094	3.42 ± 0.25	0.0790 ± 0.0013	5.82 ± 0.10	2.99 ± 0.38	0.1005 ± 0.0038

Seed treatment with the growth regulators Albit, H_2O_2 and ScA increased hypocotyl length in seedlings grown in the light by 28.64, 13.44 and 9.88 %, respectively, root length by 54.82, 50 and 75.88 %, respectively, and seedling biomass by 14.10, 1.28, 0.9 %, respectively.

Under dark conditions, treatment of seeds with Albit and ScA also effectively influenced morphometric parameters and increased hypocotyl length by 16.01 and 1.31 % compared to control, respectively, root length by 24.78 and 56.19 %, respectively, and seedling weight by 11.67 and 2.99 %, respectively. At the same time, H_2O_2 treatment reduced hypocotyl length by 4.9 % compared with control.

Remarkably, under dark conditions, hypocotyl length in control samples of amaranth seedlings was 141.9 % longer than in control samples grown under light conditions.

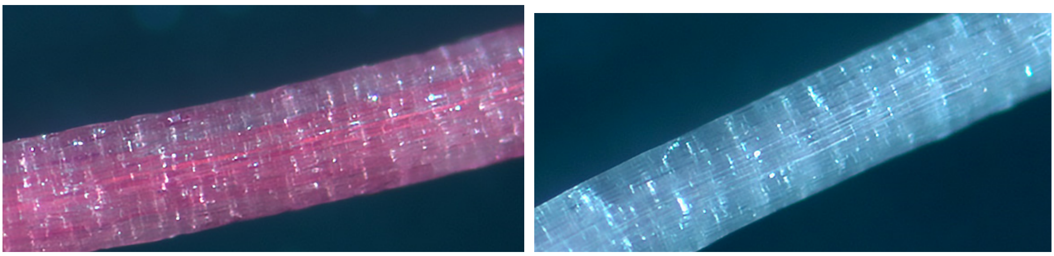
In our study, etiolated seedlings of amaranth cultivar 'Valentina' formed long hypocotyl and yellow-pink cotyledon leaves, which, when visually assessed, did not open and were smaller than the leaves of seedlings grown in the light (Fig. 1, 2).



a b

Fig. 1. Cotyledon leaf of 7-day-old seedling of amaranth cultivar 'Valentina' grown under light (a) and dark conditions (b)

Source: made by authors



a b

Fig. 2. Hypocotyl of 7-day-old seedling of amaranth cultivar 'Valentina' grown under light (a) and dark conditions (b)

Source: made by authors

Effect of low positive temperature on amaranthine and photosynthetic pigment content in light and etiolated seedlings. The study revealed an increase in amaranthine content under the action of low positive temperature in all seedlings grown under light and dark conditions. At the same time, different levels of amaranthine accumulation under hypothermia depending on plant growth regulator were observed (Table 2).

Table 2

Amaranthine content, mg/g FW, in light and etiolated seedlings of amaranth cultivar 'Valentina' grown from seeds treated with growth regulators at low positive temperature 2 °C

Variant	Light conditions		Dark conditions	
	T_{23}	T_2	T_{23}	T_2
H_2O (Control)	0.385 ± 0.014	0.395 ± 0.010	0.066 ± 0.003	0.118 ± 0.005
Albit	0.340 ± 0.008	0.519 ± 0.008	0.058 ± 0.003	0.130 ± 0.005
Succinic acid	0.380 ± 0.012	0.406 ± 0.09	0.093 ± 0.002	0.136 ± 0.006
H_2O_2	0.400 ± 0.011	0.480 ± 0.008	0.079 ± 0.004	0.140 ± 0.006

In de-etiolated seedlings, hypothermia increased amaranthine content in the control as well as in the seedlings grown from seeds treated with ScA, H_2O_2 and Albit by 2.6, 6.84, 20 and 52.65 %, respectively, and in etiolated seedlings — by 78.79, 46.24, 77.22 and 124.14 %, respectively. At the same time, in the control variants in etiolated seedlings, amaranthine content was lower by 82.86 % than in the de-etiolated seedlings.

It is known that betacyanins are photoprotective compound closely related to chilling stress [13]. The increase in amaranthine biosynthesis under hypothermic conditions suggests that this pigment plays important role in resistance of seedlings to chilling stress.

In etiolated seedlings, a trace content of the sum of chlorophylls a+b was found, so only the total content of chlorophylls in de-etiolated seedlings was presented. The action of low-temperature stress reduced the sum of chlorophylls a and b content in de-etiolated seedlings, in control and in ScA treatments, by 9.84 and 3.13 %, respectively (Table 3).

Table 3

Total chlorophyll a+b content in de-etiolated seedlings of amaranth cultivar 'Valentina' treated with plant growth regulators at low positive temperature 2 °C

Variant	Chlorophyll a+b, mg/g FW	
	T_{23}	T_2
H_2O (Control)	0.315+0.007	0.284 ± 0.005
Albit	0.267 ± 0.005	0.325 ± 0.006
Succinic acid	0.320 ± 0.012	0.310 ± 0.0010
H_2O_2	0.321 ± 0.011	0.337 ± 0.009

It is possible that the decrease in chlorophyll content under low-temperature stress may be partially related to the disruption of protochlorophyllide biosynthesis or to the inhibition of 5-aminolevulinic acid biosynthesis [14]. It is known that low-temperature stress induces lipid oxidation in membrane, which leads to the ROS formation, mainly in plastids. Subsequently, ROS oxidize photosynthetic pigment, reducing chlorophyll content [15].

However, in seedlings which seeds were treated with H_2O_2 and Albit, we found an increase in total chlorophyll content by 4.98 and 21.71 %, respectively (see Table 3). Apparently, degree of chlorophyll resistance to hypothermia in seedlings can be determined by concentration and type of growth regulator. Thus, low concentration of exogenous H_2O_2 regulates physiological processes including photosynthesis, increasing stability of photosynthetic pigments including carotenoids [16].

In chloroplasts, carotenoids act as auxiliary light-collecting pigments that direct excess energy from chlorophylls to protect against photo-oxidative damage [17].

In our experiments on de-etiolated seedlings, ambiguous data were obtained. Under hypothermic conditions, carotenoid content decreased in de-etiolated seedlings which seeds were treated with ScA by 11.11 % and in controls — by 13.76 %, while in seedlings which seeds were treated with H_2O_2 and Albit, pigment amount increased by 5.41 and 19.33 %, respectively (Table 4).

Table 4

Total carotenoid content, mg/g FW, in light and etiolated seedlings of amaranth cultivar 'Valentina' treated with growth regulators at low positive temperature 2 °C

Variant	Light conditions		Dark conditions	
	T_{23}	T_2	T_{23}	T_2
H_2O (Control)	0.138 ± 0.004	0.119 ± 0.003	0.024 ± 0.002	0.041 ± 0.001
Albit	0.119 ± 0.002	0.142 ± 0.005	0.022 ± 0.001	0.049 ± 0.002
Succinic acid	0.135 ± 0.007	0.120 ± 0.004	0.029 ± 0.003	0.043 ± 0.005
H_2O_2	0.148 ± 0.003	0.156 ± 0.004	0.031 ± 0.004	0.043 ± 0.001

At the same time, in etiolated seedlings under low positive temperatures, carotenoid content increased in all seed treatments: in the control — by 70.83 %, in treatments with Albit — by 122.73 %, ScA — by 48.28 %, H_2O_2 — by 38.71 %. It was noted that etiolated seedlings accumulated significantly less carotenoids compared with de-etiolated seedlings at both optimal and low temperatures. This may be due to the fact that carotenoid biosynthesis in etiolated seedlings is limited by the presence of metabolic precursors [18].

We found a strong activation of carotenoid biosynthesis in all treatments when exposed to light at optimal temperature. Apparently, etioplastic carotenoids contribute to adaptation of etiolated seedlings to light. In addition, regulation of carotenoid formation in the dark may allow etiolated seedlings to optimize transition to photosynthesis after light. Therefore, the light-induced deetiolation process of amaranth seedlings involves formation of high levels of carotenoids, chlorophylls and amaranthine to maintain photosynthetic and defense responses.

Under hypothermic conditions, increased content of the sum of chlorophylls as well as carotenoids in amaranth seedlings grown from seeds treated with H_2O_2 and Albit indicates the increased stability of photosynthetic pigments and, consequently, of photosynthetic apparatus.

Effect of low positive temperature on content of amaranthine antioxidant and photosynthetic pigments in cotyledon leaves of de-etiolated seedlings grown from seeds treated with growth regulators. When studying amaranthine accumulation in cotyledon leaves of de-etiolated seedlings in response to low-temperature stress, it was found that amaranthine content increased, but its amount depended on the treatment variant. Thus, in the control and when seeds were treated with H_2O_2, ScA and Albit, amaranthine content under hypothermia increased by 12.46, 35, 41.29 and 44.41 %, respectively (Table 5).

Table 5

Content of amaranthine and photosynthetic pigments: chlorophylls and carotenoids in de-etiolated seedlings treated with growth regulators at low positive temperature

Variant	Amaranthine, mg/g FW		Chlorophyll a+b, mg/g FW		Carotenoids, mg/g FW	
	T_{23}	T_2	T_{23}	T_2	T_{23}	T_2
H_2O (Control)	0.610 ± 0.010	0.686 ± 0.009	0.667 ± 0.009	0.657 ± 0.012	0.266 ± 0.009	0.276 ± 0.007
Albit	0.599 ± 0.009	0.865 ± 0.014	0.708 ± 0.012	0.750 ± 0.014	0.290 ± 0.010	0.314 ± 0.006
Succinic acid	0.603 ± 0.012	0.852 ± 0.009	0.693 ± 0.010	0.760 ± 0.010	0.278 ± 0.005	0.321 ± 0.007
H_2O_2	0.618 ± 0.014	0.838 ± 0.010	0.693 ± 0.009	0.777 ± 0.007	0.283 ± 0.008	0.335 ± 0.009

Amaranthine is a pigment that is essential for homeostasis under abiotic stress. Significant accumulation of betacyanin accumulates in the upper and lower epidermis, in palisade and spongy mesophyll cells, as well as in guard cells [19].

Chlorophyll content under low positive temperature conditions decreased only in cotyledon leaves of control seedlings by 1.5 %, while treatment of seeds with Albit, ScA and H_2O_2 increased chlorophyll content in seedlings by 5.93, 9.67 % and 12.12 %, respectively.

Wittayathanarattana et al. concluded that the effect of short-term positive low temperature stress on amaranth root system limits photosynthesis, which depletes plant tissue resources and forces plants to conserve critical nutrients for survival. Chlorophyll may be less necessary under conditions of limited resources and excessive ROS compared to amaranthine and carotenoids [15].

Carotenoids are pigments accumulated in chloroplasts and are crucial for photoprotection, light trapping and stabilization of photosynthetic activity [20], and have high antioxidant capacity by removing singlet oxygen and peroxyl radicals [21].

Under hypothermia, increase in carotenoid levels was observed in all variants: by 3.76 % — in the control, by 8.27 % — in treatment with Albit, by 15.47 % — in treatment with ScA and by 18.37 % — in treatment with H_2O_2.

Under conditions of low positive temperature, amount of antioxidant amaranthine and carotenoids in cotyledon leaves significantly increased in seedlings treated with Albit, H_2O_2 and Sc A. Thus, all used growth regulators trigger or at least maintain the system of antioxidant protection in light and etiolated seedlings of amaranth cultivar 'Valentina' under low positive temperatures.

Conclusions

Pre-sowing treatment of amaranth seeds with growth regulators not only increased seed quality, but also changed — increased or decreased antioxidant capacity of seedlings, as well as growth processes compared with control. Low positive temperature induced amaranthine synthesis in light and etiolated seedlings in all types of seed treatments with growth regulators, whereas carotenoid synthesis increased in de-etiolated seedlings only when seeds were treated with H_2O_2 and Albit, and in ethiolated seedlings — when seeds were treated with Albit, ScA and H_2O_2.

According to the literature data and the results of our study, it can be assumed that hypothermia induces excess of ROS molecules in cells, which exhibit both the properties of toxic metabolic products and signaling molecules, being involved in the processes leading to increase in seedling resistance to stress. The resistance of amaranth seedlings is expressed through the amount of induced amaranthin molecules formed after low-temperature stress exposing. The level of increase in amaranthine content in cotyledon leaves after low temperature stress may indicate the different ability of seedlings to induce the maximum amount of antioxidants for a given treatment. Compared to the control, the amaranthine synthesis system gives greater resistance to hypothermia to seedlings which seeds were treated with growth regulators.

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Влияние низкой положительной температуры на формирование антиоксидантной системы световых и этиолированных проростков *Amaranthus tricolor* L., выращенных из семян, обработанных регуляторами роста

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Аннотация. В Нечерноземной зоне России возвратные весенние холода до 1–2 °C могут вызвать повреждения и гибель проростков теплолюбивого растения — амаранта. Недорогим и эффективным методом для снижения негативного действия гипотермии на прорастание семян является предпосевная обработка семян регуляторами роста. Цель исследования — изучение влияния низкотемпературного стресса на этиолированные и световые проростки амаранта сорта Валентина (*A. tricolor* L.), выращенные из семян, обработанных регуляторами роста. Для предпосевной обработки семян использовали водные растворы Альбита — 1 г/л, перекиси водорода (H_2O_2) — 5 мМ и янтарной кислоты (ЯК) — 500 мг/л. Семена проращивали в торфяных горшках при температуре 23 ± 2 °C (T_{23}) в течение 7 суток. На 7-й день торфяные горшки с проростками, выращенными на свету и в темноте, перемещали в термостат при температуре 2,0 ± 0,5 °C (T_2) на 8 часов. Определение количества амарантина, хлорофиллов и каротиноидов проводили по общепринятым методикам. Предпосевная обработка семян регуляторами роста Альбит, H_2O_2 и ЯК увеличивала длину гипокотиля, длину корня и биомассу световых и этиолированных проростков. Действие низких положительных температур повышало содержание амарантина и каротиноидов, однако, снижало содержание хлорофиллов. Показано, что все использованные регуляторы роста: H_2O_2, Альбит и ЯК — запускают либо поддерживают систему антиоксидантной защиты световых и этиолированных проростков амаранта сорта Валентина при действии низких положительных температур.

Ключевые слова: сорт Валентина, амарантин, фотосинтетические пигменты, абиотический стресс, низкотемпературный стресс, хлорофилл

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