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THE EFFECT OF AMARANTHINE ON THE STRESS-RESISTANCE OF TOMATOES (*Lycopersicon esculentum* Mill.) INVADED BY THE ROOT-KNOT NEMATODE (*Meloidogyne incognita*)

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Abstract

Root-knot nematodes of the genus *Meloidogyne* are sedentary parasites that infect the root system of plants, the annual damage from which in the world exceeds 80 billion EUR per year. Infection of plants with these nematodes causes biogenic stress, which is associated with changes in the respiratory processes of plants, a decrease in photosynthesis, the appearance of highly reactive oxygen radicals in the tissues with the formation of toxic intermediate products that cause oxidative stress. The high biological activity of amaranthine isolated from *Amarathus tricolor* L. combined with antioxidant properties, show the promise of its study as a factor resistance to stress of plant during invasion by parasitic nematodes. In this work, we first showed the adaptogenic properties of amaranthine towards tomato plants infected with root-knot nematode. We investigated the effect of the amaranthine beta-cyanine pigment extracted from *A. tricolor* on the parasite-host system of the tomato *Lycopersicon esculentum* Mill. and root-knot nematode *Meloidogyne incognita* (Kofoid & White, 1919) Chitwood 1949. Aqueous solutions of the amaranthine in concentrations from 0.1 to 2.0 mg/ml were tested. When studying the effect of amaranthine on nematodes in vitro, it was found that the analyzed compound has a nematostatic effect in the range of concentrations from 1.0 mg/ml and lower. The 2.0 mg/ml concentration was lethal for *M. incognita*. The effect of amaranthine on biometric and photosynthetic characteristics of tomato plants infected with the root-knot nematode *M. incognita*, and morphological and physiological parameters of nematodes from plants treated with amaranthine were evaluated in a lab greenhouse. Before planting, the seeds were soaked in amaranthine solutions (0.5 and 1.0 mg/ml) for 3 hours, and then seedlings reached the phase of 3-4 true leaves were sprayed with solutions at the same concentrations and infected with nematodes (three thousand larvae per plant). This experiment revealed stimulating effect of the amaranthine in the tested concentrations on plant development. The treated seeds sprouted 2-3 days earlier than the control seeds, the average root length of the seedlings treated with the 1.0 mg/ml preparation on day 7 significantly differed from the control (18 %, $p \le 0.05$). The effect of amaranthine on nematodes was evaluated on day 40 after invasion. A comparative analysis of nematodes from the test and control plants showed that the plant treatment with 0.5 and 1.0 mg/ml aqueous amaranthine solutions led to a decrease in the number of nematodes on the roots. The number of sexually mature females per gram of roots under the treatment with 0.5 and 1.0 mg/ml solutions was 2.1 and 1.3 times less compared to the control. Female nematodes from such plants were 1.2 times smaller in both variants; the number of eggs was also 15-20 % less ($p \le 00.05$) as compared to control. The complex of protective mechanisms in infected tomato plants induced by the action of exogenous amaranthine includes stabilization of photosynthetic processes disturbed by the nematode, accumulation of carotenoid antioxidants, switching of non-cyclic electron transport from water in the Photosystem I to pseudocyclic, stimulation of tomato plant growth. Out findings indicate that amaranthine exhibits adap-

togenic properties associated with the weakening of negative biochemical and functional changes in plants during nematode invasion. Amaranthine can be proposed as a novel biogenic inducer which provides protective effect due to activation of non-specific plant response to biotic stress under pathogen invasion in greenhouse conditions, and also possesses growth-promoting properties.

Keywords: amaranthine, antioxidant, adaptogen, *Amaranthus tricolor* L., variety Valentine, *Meloidogyne incognita*, tomatoes, chlorophyll, carotenoids, oxidative stress, electron transport

As per modern concepts, plant pathogens are stress factors that cause complex protective reactions of plants, including both non-specific (common to different types of stressors) and specific components [1]. At the same time, biogenic stress induced by plant pathogens has a number of features that distinguish it from stress caused by abiogenic extreme factors. This fully applies to plant-parasitic nematodes which exert physical and chemical multifactorial effect on plants [2].

Nematodes, especially sedentary plant-parasitic nematodes which include the *Meloidogyne* root-knot nematodes, are dangerous parasites of agricultural plants that cause damage of over 80 billion euros per year [3]. Symptoms of pants invasion are like those characteristic of the effects of such extreme factors as drought, cold, and mineral starvation. Nematode invasion affects gas exchange in respiration, leads to a decrease in photosynthesis and the appearance of highly reactive oxygen species in the tissues with the production of toxic intermediate compounds that cause oxidative stress [4-6].

The substances of specialized metabolism play an important role among the factors contributing to the survival of plants under biogenic stress, including those caused by damage by plant-parasitic nematodes. These compounds can act on the pathogen as toxins, affect growth, larvae hatching and development; these metabolites are known to possess antifeedant and adaptogenic properties, as well as ability to change intracellular membranes and to normalize photosynthesis and metabolism intensity in infected plants [7-10].

Amaranth is one of the crops for which a rich composition of low molecular weight metabolites, the protectors and immunostimulants of living organism, are characteristic [11, 12]. High content of deterrents, including the amaranthine alkaloid, makes amaranth unattractive for many plan pathogens [13]. Data on the damage of amaranth plants by plant nematodes are scarce and contradictory. Testing 10 species of amaranth for resistance to gall nematodes in South Africa reveal no samples resistant to *Meloidogyne incognita* race 2 and *Meloidogyne javanica* [14]. However, there is evidence of high resistance of amaranth hybrids to the root-knot nematode [15]. Introducing amaranth plants into the crop rotation to control the root-knot nematode *M. javanica* on nightshade and pumpkin crops gave a positive result [16]. The inconsistency of the data, apparently, is associated with a wide variety of species-specific properties, including the composition and content of secondary metabolites in plants of this genus which comprises up to 90 species.

The violet-red beta-cyanine pigment amaranthine outstands of the metabolites of red-colored *Amaranthus tricolor* L. which reduce the effects of plant oxidative stress. Amaranthine can neutralize superoxide anions $O_2^{\bullet-}$), free radicals and chelate Fe^{2+} ions [17]. Exogenous amaranthine increases electron transfer along a non-cyclic pathway (Hill reaction) in isolated chloroplasts [18]. Amaranthine participates in protective and adaptive response to photostress, stimulates plant growth and seed germination, and shows a positive effect under extreme temperatures and drought conditions [12]. Amaranthin also showed a protective effect upon treatment of cucumber leaves affected by thrips [13].

High biological activity of amaranthine of *A. tricolor* combined with antioxidant and antifeedant properties makes this metabolite a promising factor in

plant resistance to stress during invasion by parasitic nematodes

In this work, the adaptogenic effect of amaranthine during nematode invasion in tomato plants is first shown, which is expressed in the activation of energy metabolism and recovery processes.

Our goal was to evaluate the effect of amaranthine on the morphophysiological and photosynthetic parameters of tomato plants under root-knot nematode *Meloidogyne incognita* invasion and to evaluate morphological and physiological parameters of nematodes from plants treated with amaranthine.

Materials and methods. The investigations were carried out in 2016-2017 on Carlson tomato (*Lycopersicon esculentum* Mill.) heterotic hybrid F_1 with a 30% resistance to *Meloidogyne incognita* (Kofoid & White, 1919) Chitwood 1949. Amarantin was extracted from freshly picked leaves of amaranth (*A. tricolor* L.) Valentina varieties (bred in the All-Russian Research Institute of Selection and Seed Production of Vegetable Crops, authors V.K. Gins, P.F. Kononkov, M.S. Gins) [12]. In the experiments, freeze-dried amaranthine powder was used.

The effect of aqueous solutions (2.0; 1.0; 0.75; 0.5 mg/ml) of amaranthine on the viability of nematodes was assessed in vitro by motor activity of II instar larvae. Nematodes placed in distilled water served as a control. The experiment was repeated thrice for each variant (20 larvae each). Root-knot nematodes initially collected in the Teplichny state farm (Moscow) were thereafter lab-cultivated on roots of a susceptible tomato variety. Larvae were obtained from isolated egg sacs of nematodes that live in the roots of infected tomato plants [19]. Larvae were incubated in a thermostat in a humidity chamber at 25 °C, in 24 and 48 hours the motility of individuals was evaluated.

The effect of various amaranthine concentrations (1.0; 0.5 and 0.1 mg/ml) on tomato seed germination was determined in vitro. The seeds were soaked in aqueous solutions of the substance for 3 hours, and the seeds soaked in distilled water were a control (20 seeds per each variant). Seeds were germinated in a ~~a~~ humidity chamber at 25 °C. The seedling development was evaluated in 3, 5 and 7 days.

The effect of amaranthine on tomatoes and root-knot nematode was investigated in a lab greenhouse. Before planting, the seeds were soaked in amaranthine solutions (0.5 and 1.0 mg/ml) for 3 hours. At 3-4 true leaves, the seedlings were sprayed with amaranthine solutions in the same concentrations and simultaneously infected with a nematode (3 thousand larvae per plant). The control was healthy and invaded plants treated with water. Plants were grown in separate 1 l flowerpots (10 plants per variant). The effectiveness of amaranthine was evaluated on day 40 after root invasion with nematodes. Root infestation estimates corresponded to 5-point scale (1-10% for 1 point; 11-35% for 2 points; 36-70% for 3 points; 71-100% for 4 points). Also the estimates were the number of stem swellings (galls per 1 g root), the weight of plant aerial parts and roots, and morphophysiological indicators of the state of the parasite population, i.e. the size of the females and their fecundity, eggs per ootheca [20].

Chlorophylls and carotenoids were measured by absorption spectra of leaf ethanol extracts [21] on day 10 and day 40 after the plant invasion with root-knot nematodes and foliar application of 0.5 mg/ml amaranthine aqueous solution to the invaded plants (Solar PB2201 spectrophotometer, ZAO SOLAR, Belarus).

Chloroplasts were isolated from leaves (1 g) triturated in 0.3 M sucrose; 0.1 M NaCl; 0.01 M $MgCl_2$; 0.05 M Tris buffer; 1% bovine serum albumin (BSA) (pH 7.5). The homogenate was filtered through nylon net and clarified for 3 min at 250 g (MPW 251 centrifuge, MPW Med. Instruments, Poland) to precipitate intact cells and cell large fragments, with repeated centrifugation of

the supernatant at 1000 g for 10 min. The precipitate of chloroplasts was suspended in 0.3 M sucrose, 0.025 M NaCl, 0.01 M $MgCl_2$; 0.05 M Tris buffer (pH 7.5).

The potency of electron transport chain (ETC) to transfer water electrons to potassium ferricyanide or molecular oxygen was assayed by the rate of O_2 reduction under separate functioning of each of these acceptors. O_2 photoreduction was determined by absorption with the Möller reaction reagent (adrenaline), which is capable of interaction with the superoxide anion radical on the reduction part of the photosystem. Adrenaline (0.3 mM) (FSUE Moscow Endocrine Plant, Russia) or potassium ferricyanide (0.5 mM) was added to the reaction mix. The oxygen concentration was measured amperometrically (a Universal polarograf OH-105 polarograph, Radelkis, Hungary) in a 1.2 ml cell with a closed platinum electrode, the reaction mix pH 7.8. The chloroplast suspension was illuminated with white light (LETI-60, Kazan Optical and Mechanical Plant OJSC, Russia). The concentration of chlorophyll was calculated using Arnon's formula.

Data were processed using analysis of variance (ANOVA) with STATISTICA 6.0 software (StatSoft, Inc., USA). The tables show the mean values (*M*) and standard errors of the means (±SEM). Significance of differences was evaluated by Student *t*-test. Differences were considered statistically significant at $p \leq 0.05$.

Results. The seed treatment with 1.0 and 0.5 mg/ml amaranthine stimulated germination. Seeds in the experiment germinated 2-3 days earlier than the control. On days 5 and 7, the average root length of seedlings when 1.0 mg/ml was applied exceeded the control by 10 and 18% ($p \leq 0.05$) (Table 1), cotyledon leaves also appeared and developed earlier.

1. Germination and root formation in tomato (*Lycopersicon esculentum* Mill.) heterotic F_1 hybrid Carlson after soaking seeds in different concentrations of amaranthine (*n* = 20, in vitro)

Variant	Days after seed soaking				
	day 3	day 5		day 7	
	germinated seeds, %	germinated seeds, %	root length, cm (*M*±SEM)	germinated seeds, %	root length, cm (*M*±SEM)
0.1 mg/ml	0	40	0.95±0.220	100	3.34±0.510
0.5 mg/ml	0	50	1.22±0.280	100	2.86±0.090
1.0 mg/ml	40	60	1.55±0.430	100	3.49±0.280*
Control (water)	0	40	1.40±0.470	100	2.96±0.460

* Differences with control are statistically significant at $p \leq 0.05$.

2. The number of moving II instar larvae root-knot nematode (*Meloidogyne incognita*) exposed to different concentrations of amaranthine (*M*±SEM)

Variant	Hours after exposure			At the end of the test when transferred to water
	0	24	48	
0.5 mg/ml	20±0.6	20±0.6	11±1.8	19±0.6
0.75 mg/ml	20±1.2	18±3.0	9±3.6	17±3.0
1.0 mg/ml	20	2±1.2	0	15±4.1
2.0 mg/ml	20	0	0	2±1.2
Control (water)	20	20	19±0.6	19±0.6

We also revealed the nematostatic effect of 0.5 to 1.0 mg/ml amaranthine (Table 2). Larvae in these solutions lost their mobility, but restored it after keeping in distilled water. In a 1.0 mg/ml amaranthine, loss of nematode mobility occurred after 24 hours. Nematode exposure to 0.5 mg/ml amaranthine solution for 48 hours resulted in a mobility loss of ~ 50% larvae. Amaranthine concentration of 2 mg/ml was lethal for larvae.

Similar properties were previously noted for physostigmine alkaloid with

a structure similar to amaranthine. This compound extracted from *Calabar bean* (*Fabaceae*) had a nematostatic effect on the migrating nematode *Ditylenchus dipsaci* at a concentration of 1.0 mg/ml. Pretreatment of pea seedlings with physostigmine sulfate (0.03 mg/ml) significantly protected plants from nematode infestation. It is possible that the mechanism of action of amaranthine on nematodes is similar to the action of physostigmine [22].

Foliar treatment of vegetative plants with 0.5 and 1.0 mg/ml amaranthine led to a decrease in the number of parasitic nematodes on the roots, and also influenced their morphophysiological parameters. On plants treated with 0.5 and 1.0, respectively mg/ml amaranthine, the number of sexually mature females per 1 g root on day 40 was 2.1 and 1.3 times less, respectively, the control. Female nematodes from the roots of the treated plants were 1.2 times smaller, and the number of eggs per ootheca was 15-20% less as compared to the control (Table 3).

3. Growth of invaded tomato (*Lycopersicon esculentum* Mill.) heterotic F_1 hybrid Carlson and morphophisiological parameters of root-knot nematode (*Meloidogyne incognita*) on day 40 after spraying vegetating plants with amaranthine (n = 10, M±SEM, pot test)

Variant	Weight, g		Infection ball	Females per 1 g root	Female size (length × wigth), mm^2	Eggs per ootheca
	aerial parts	roots				
Amaranthine, 0.5 mg/ml	32±1.1*	2.8±0.40	2	324±39.0*	0.300±0.0100*	93±12.0*
Amaranthine, 1.0 mg/ml	27±2.4	2.9±0.60	3	544±54.0	0.298±0.0070*	90±17.0*
Control (invaded plants. water)	24±1.1	3.1±0.70	4	684±46.0	0.354±0.0110	146±22.0
Control (healthy plants. water)	29±2.8	2.4±0.30	–	–	–	–

N o t e. Dashes mean absence of the data.
* Differences with the invaded control are statistically significant at $p \le 0.05$.

The infection ball in plants treated with amaranthine was significantly lower than in control. Especially effective concentration was 0.5 mg/ml, resulting 2 times less gall number compared to the roots of control plants. Weight of the aerial parts of invaded plants treated with 0.5 and 1.0 mg/ml amaranthine exceeded the control by 32% ($p \le 0.05$) and 10%, respectively. The weight of roots in infected plants, on which a significant number of galls were found, was noticeably greater than in healthy ones. Their weight ratio to the aboveground organs (stem and leaves) also differed from that in healthy plants. Under the influence of amaranthine, the ratio of root to aboveground parts was comparable to that of uninfected plants, which indicates the normalization of metabolic processes and the physiological state of tomatoes.

4. Dynamics of chloroplast pigments in leaves of tomato (*Lycopersicon esculentum* Mill.) heterotic F_1 hybrid Carlson after treatment with amaranthine at root-knot nematode (*Meloidogyne incognita*) invasion (n = 10, M±SEM, pot test)

Variant	Day 0		Day 10		Day 40	
	chlorophylls a + b	carotenoids	chlorophylls a + b	carotenoids	chlorophylls a + b	carotenoids
Amaranthine, 0.5 mg/ml	2.35±0.087	0.80±0.025	2.63±0.121	0.90±0.018	2.31±0.074*	0.77±0.011*
Control (invaded plants. water)	2.29±0.030	0.79±0.042	2.50±0.089	0.83±0.045	2.11±0.144	0.60±0.035
Control (healthy plants. water)	2.30±0.139	0.81±0.035	2.65±0.145	0.91±0.057	2.40±0.108*	0.80±0.014*

* Differences with the invaded control are statistically significant at $p \le 0.05$.

Important indicators of plant physiological status include the content of photosynthetic pigments in chloroplasts. On day 10 in the leaves of tomato plants invaded with nematodes, the chlorophylls increased by 13%, carotenoids

by 10% (Table 4). Perhaps the increase in the content of photosynthetic pigments was a response to oxidative stress caused by the gall nematode invasion into the roots. The total content of chlorophylls and carotenoids in healthy and amaranthine-treated plants was almost the same. On day 40, a decrease in leaf photosynthetic pigments occurred in all studied plants ($p \leq 0.05$). The content of chlorophylls in nematode-invaded plants decreased by 12%, carotenoids by 15%, and in the invaded plants after amaranthine treatment these indicators were 8 and 5% lower, respectively, compared to healthy plants.

The lower amount of chlorophylls and carotenoids in chloroplasts upon root-knot nematode infestation (biogenic stress) indicates changes in the photosynthetic electron transport chain in tomato C3 plants. In photosynthetic systems, in addition to the main chain of electron transfer from water to NADP or an artificial acceptor (non-cyclic electron transport), the chain of pseudocyclic electron transport works as $H_2O \rightarrow PSII \rightarrow PSI \rightarrow O_2 \rightarrow H_2O$. Pseudocyclic transport acts as an alternative electron transfer pathway, which leads to the reduction of molecular oxygen and the formation of superoxide anion and H_2O_2 [23]. It is known that the enhancement of electron transfer to oxygen can occur under a decrease in the oxidized NADP or inhibition of dark photosynthesis reactions, as well as under the adverse factors. For example, at water deficit in leaves, in chloroplasts there is a redistribution of flow of electrons associated with the reduction of CO_2 and O_2 [24, 25].

5. Non-cyclic (Hill reaction) **and pseudocyclic** (Møller reaction) **electron transport in tomato (*Lycopersicon esculentum* Mill.) heterotic F_1 hybrid Carlson at root-knot nematode (*Meloidogyne incognita*) invasion (day 40) after treatment with amaranthine** ($n = 3$, $M \pm$SEM, pot test)

Variant	Hill reaction, μmol $O_2 \cdot mg^{-1}$ chlorophyll $\cdot h^{-1}$	Møller reaction, μmol $O_2 \cdot mg^{-1}$ chlorophyll $\cdot h^{-1}$
Amaranthine, 0.5 mg/ml	26±3.0*	17±2.0*
Control (invaded plants. water)	13±2.0*	22±3.0*
Control (healthy plants. water)	64±4.0	12±2.0

* Differences with the healthy control are statistically significant at $p \leq 0.05$.

In chloroplasts from the leaves of invaded plants, electron transfer to molecular oxygen along the pseudocyclic path increased sharply, up to 67% at $p \leq 0.05$, and decreased along the non-cyclic path, up to 80%, compared to the uninvaded plants (Table 5). The 0.5 mg/ml amaranthine solution applied to leaves of the invaded plants led to a 36% decrease in the electron transfer to molecular oxygen compared to healthy plants, and, therefore, in the chloroplasts electron transport via non-cyclic path (Hill reaction) increased up to 30%.

Amaranthine has an auxin-like effect on plants invaded by root-knot nematodes, including stimulation of aboveground mass and root growth, the influence on the content of chlorophylls and carotenoids, and also on the electron transfer via non-cyclic and pseudocyclic pathways. This fact indicates that the amaranthine molecule is unique in its functional properties [12, 26].

Infestation of tomato plants by root-knot nematodes can weaken photosynthesis, including primary processes in thylakoid membranes. When oxidative stress strengthens, photooxidation in chloroplasts intensifies, which probably causes the electron flux in the PSI region to be switched from non-cyclic to pseudocyclic pathway of transport electrons from water. Generation of reactive oxygen species (ROS), i.e. a superoxide radical and H_2O_2, is associated with pseudocyclic electron transport, which enhances oxidative stress in chloroplasts. Free radical oxidation leads to destruction of organic molecules, which may result in metabolic disturbance and even death of plants [27]. The natural antioxi-

dant system which includes low- and high-molecular-weight compounds, takes part in the regulation of the ROS amount. We revealed that in invaded tomato plants, the complex of protective mechanisms induced by exogenous amaranthine includes the accumulation of antioxidants carotenoids, switching non-cyclic electron transport from water in the PSI region to the pseudocyclic pathway, and stimulation of plant growth. All this in general leads to an increase in the resistance of tomato plants to root-knot nematodes.

Similar results were reported about the action of natural adaptogens, the furostanol glycosides extracted from *Dioscorea deltoidea* Wall cell culture, on the *M. incognita*—tomato parasite-~~and-~~host system. Application of furostanol glycosides to tomato seeds and vegetating plants markedly reduced susceptibility to parasitic nematodes [7]. The preparation influenced pigment pool of the photosynthetic apparatus, the peroxidase activity, and stimulated lipid peroxidation. The pattern of changes in the chloroplast pigment composition revealed upon treatment with amaranthine and furostanol glycosides indicates that these compounds support cell homeostasis via plant immunity stimulation.

Note that the search for natural compounds with nematicidal properties is a fairly wide research area. Data on the effect of plant-derived substances of different classes on parasitic nematodes and plant resistance are given in the Chitwood's review [10]. The induced plant systemic resistance to root-knot nematodes was noted for aqueous extracts from fresh leaves of lemon grass *Cymbopogon flexuosus* Steud. [28] and upon treating the aerial parts of plants with an oil extract from of *Argemone mexicana* L. seeds [29]. Watercress, as well as ordinary horseradish exhibit antagonistic properties against *M. incognita*. Preparations based on these plants have a high nematostatic activity, namely inhibit hatching of larvae from eggs, paralyze invasive larvae, act also as stimulants and can stabilize cultivated plant development. Preparations containing substances of specialized plant metabolism with nematicidal properties positively influence growth and photosynthesis of plants and negatively affect gall nematode development.

Thus, amaranthine has adaptogenic properties, namely weakens negative biochemical and functional changes in tomato plants under stress caused by nematode invasion, and activates synthesis of the compounds which provide improved energy metabolism and recovery processes. The 1.0 and 0.5 mg/ml amaranthine concentrations, on the one hand, stimulate tomato seed germination, plant growth and synthesis of chlorophylls and carotenoids, and, on the other hand, inhibit the mobility of nematode larvae and their development in plants, including morphometric and population indicators. Therefore, amaranthine can be a novel biogenic inducer which is capable of activating general non-specific stress response systems at plant pathogen invasions. This bioagent can provide both protective and growth-promoting effect in greenhouses.

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